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Female flowers and systematic position of Picrodendraceae (Euphorbiaceae s.l., Malpighiales)

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Abstract. This is the first comparative study of floral structure of the recently established new family Picrodendraceae (part of Euphorbiaceae s.l.) in Malpighiales. Nine species of eight (out of ca. 28) genera were studied. Female flowers are mainly completely trimerous, and in such flowers the perianth consists of one or two whorls of sepals. A floral disc (which probably functions as a nectary) is mostly present. The free parts of the carpels are simple (unbranched) in all ten species studied. Each carpel contains two crassinucellar, anatropous or hemitropous, epitropous (antitropous) ovules, which are covered by a large obturator. The inner integument is thicker than the outer (equally thick in two species studied), and commonly both integuments form the micropyle. In mature ovules the vascular bundle commonly branches in the chalaza, with the branches extending to the base of the inner integument but not entering it. A nucellar cap and, less often, a nucellar beak is formed. Floral structure supports the close relationship of Picrodendraceae with Phyllanthaceae and Euphorbiaceae s.str. within Malpighiales, as suggested (but not yet strongly supported) by some recent published molecular analyses. These three families share a unique combination of characters, including (1) unisexual, apetalous trimerous flowers, (2) crassinucellar ovules with a nucellar beak, (3) a large obturator, and (4) explosive fruits with carunculate seeds.

Key words: *Picrodendraceae*, Euphorbiaceae, Phyllanthaceae, Malpighiales, floral structure, perianth, gynoecium, ovules.

Introduction

Euphorbiaceae in the broad, classical sense (here referred to as 'Euphorbiaceae s.l.') are a greatly diverse group, comprising over 300 genera and about 8000 species (Webster 1994a, b; Radcliffe-Smith 2001). Various classification systems have been proposed by different authors. In the most comprehensive recent intrafamilial classification (Webster 1994a, b), five subfamilies are recognized: the uniovulate Acalyphoideae, Crotonoideae and Euphorbioideae, and the biovulate Phyllanthoideae and Oldfieldioideae. However, in molecular phylogenetic analyses, Euphorbiaceae s.l. do not form a single monophyletic group (Savolainen et al. 2000, Soltis et al. 2000, Chase et al. 2002, APG 2003), but rather form five subgroups representing three larger and two smaller clades, all in Malpighiales. The larger

clades are: (1) Euphorbiaceae s.str. (Savolainen et al. 2000, Soltis et al. 2000, Chase et al. 2002, APG 2003) (ca. 220 genera), consisting of Acalyphoideae, Crotonoideae, and Euphorbioideae, (2) Phyllanthaceae (Savolainen et al. 2000, Chase et al. 2002, APG 2003; as "Putranjivaceae" in Soltis et al. 2000) (ca. 60 genera), consisting of Phyllanthoideae, and (3) Picrodendraceae (Chase et al. 2002, APG 2003; as "Pseudanthaceae" in Savolainen et al. 2000, Soltis et al. 2000) (ca. 28 genera), consisting of Oldfieldioideae. The two smaller clades are Putranjivaceae (Chase et al. 2002, APG 2003) (4 genera) (earlier in Phyllanthoideae, Webster 1994b) and Pandaceae (Chase et al. 2002, APG 2003) (3 genera) (earlier in Acalyphoideae).

Some recent non-molecular studies also questioned the monophyly of the Euphorbiaceae s.l. based on structural features (Meeuse 1990, Huber 1991, Stuppy 1996) and assumed that they consisted of two or three unrelated groups. Meeuse (1990) positioned Phyllanthaceae close to Flacourtiaceae (Violales, Malviflorae), Picrodendraceae (as Paivaieusaceae) close to or in Sapindales (Rutiflorae), and Euphorbiaceae in Euphorbiales (Malviflorae). Huber (1991) recognized two different families, the Euphorbiaceae proper (with one ovule per carpel), which he included in Violales or Malvales, and the remainder of the Euphorbiaceae s.l. (with two ovules per carpel), which he included in Linales. Sutter and Endress (1995), in contrast, emphasized the presence of a unique character combination in the gynoecium in four of the five subgroups (Picrodendraceae not studied), thus favouring of a close relationship between these subgroups.

Despite the polyphyly of Euphorbiaceae s.l. suggested by molecular studies, they reconcile to some extent the two opposing views of non-molecular studies, in that all subclades of Euphorbiaceae s.l. are included within the new, large order Malpighiales. In the *rbc*L study by Chase et al. (2002), 16 other families are nested within the three larger clades of Euphorbiaceae s.l.: Achariaceae, Balanopaceae, Caryocaraceae, Chrysobalanaceae (incl. Dichapetalaceae, Trigoniaceae), Ctenolophonaceae, Goupiaceae, Irvingiaceae, Ixonanthaceae, Lacistemataceae, Linaceae, Ochnaceae, Rhizophoraceae (incl. Erythroxylaceae) and Violaceae. However, the relationships between all of these families were not well supported.

The most recent molecular studies appear to bring the clades of Euphorbiaceae s.l. even closer together (Wurdack et al. 2004, 2005; Samuel et al. 2005; Kathriarachchi et al. 2005). A weakly supported sister relationship between Picrodendraceae and Phyllanthaceae has appeared in several studies based on *rbc*L or *rbc*L plus two other regions (Wurdack 2002, Davis and Chase 2004, Wurdack et al. 2004). Most recently, a study based on nucleotid sequences of 4 regions retrieved a clade with Euphorbiaceae s.str. sister to a clade with Phyllanthaceae + Picrodendraceae plus only 5 other families (Ochnaceae, Medusagynaceae, Quiinaceae, Ctenolophonaceae, and the genus *Centroplacus*) (Davis et al. 2005).

A study with good resolution for the entire Euphorbiaceae s.l. is still missing but more detailed analyses are in progress (Wurdack and Davis 2005, Tokuoka and Tobe 2005). Thus, major changes to the overall topology of the major subclades of Malpighiales are to be expected.

Of the three larger clades of the classical Euphorbiaceae s.l., Picrodendraceae is the smallest (ca. 28 genera, ca. 100 species) and morphologically the least investigated. There are two structural surveys of the clade, one based on leaf and wood anatomy (Hayden 1994) and the other on pollen structure (Levin and Simpson 1994, Simpson and Levin 1994). Other related publications mainly concentrate on the structure or taxonomy of single species or genera (e.g. Forster 1995, 1997a, b; Forster and van Welzen 1999). Berg (1975) investigated the gynoecium development of two *Micrantheum* species in order to gain a better understanding of their myrmecochorous dispersal, Hakki (1985) studied the gynoecium and some embryological characters of *Picrodendron baccatum*, and Dahlgren and Van

Wyk (1988) presented a general description of *Androstachys johnsonii* including the female flowers.

For the other two larger clades, Euphorbiaceae s.str. and Phyllanthaceae, several extensive works on structural aspects were published over the past decade (e.g. Kapil and Bhatnagar 1994; Tokuoka and Tobe 1995, 1998, 2001, 2003; Jensen et al. 1994; Nowicke 1994). From these publications it appears that the female flowers are the least variable part of the plant in Euphorbiaceae s.l. Sutter and Endress (1995) found that the gynoecium of Euphorbiaceae s.str. and Phyllanthaceae has special features, which in their combination may be unique to Euphorbiaceae s.l., such as epitropous, crassinucellar ovules, protruding nucellar beaks and obturators.

In the present study the gynoecium of nine species of eight genera of the Picrodendraceae is investigated with the aim to increase our knowledge on a poorly known family and to contribute to the discussion of the inter- and intrafamiliar relationships of the Euphorbiaceae s.l.

Material and methods

The following taxa and collections were studied:

Austrobuxus megacarpus P.I. Forst., coll. P. Forster, PIF 19209, B. Hyland, B.H. 13521
Choriceras majus Airy Shaw, coll. B. Hyland, B.H. 9365
Dissiliaria baloghioides Baill., coll. P. Forster, PIF 13126 A
Dissiliaria muelleri Baill., coll. P. Forster, PIF 12713
Micrantheum hexandrum Hook.f., coll. A. Kocyan, AK 98 1007/1/02
Neoroepera banksii Benth., coll. B. Hyland, B.H. 6946
Petalostigma pubescens Domin, coll. P. Forster, PIF 14066
Sankowskya stipularis P.I. Forst., coll. B. Hyland, B.H. 13893
Whyanbeelia terrae-reginae Airy Shaw & B.Hyland, coll. P. Forster, PIF 17171

Anthetic flowers fixed in FAA and stored in 70% ethanol were used for light (LM) and scanning electron microscopy (SEM). For serial microtome sections specimens were embedded in Kulzer's Technovit (2-hydroethyl methacrylate), as described in Igersheim (1993) and Igersheim and Cichocki (1996), and sectioned with a Microm HM 335 rotary microtome and conventional microtome knife D. The 5 μm thick sections were stained with ruthenium red and toluidine blue (Weber and Igersheim 1994). All sections were mounted in Histomount. For SEM studies, specimens were dehydrated in ethanol and acetone, critical-point dried, and sputter-coated with gold. All vouchers (liquid-fixed material and permanent slides of the microtome sections) are deposited at the Institute of Systematic Botany of the University of Zurich (Z), Switzerland.

Glossary

Angiospermy types: Angiospermy (carpel closure) within angiosperms takes place in a variety of different ways, including secretion of the carpel margins and postgenital fusion of the carpel margins to varying degrees: type 1 (only secretion), type 2 (secretion and partial postgenital fusion at the periphery), type 3 (secretion and complete postgenital fusion at the periphery), type 4 (only postgenital fusion) (Endress and Igersheim 2000).

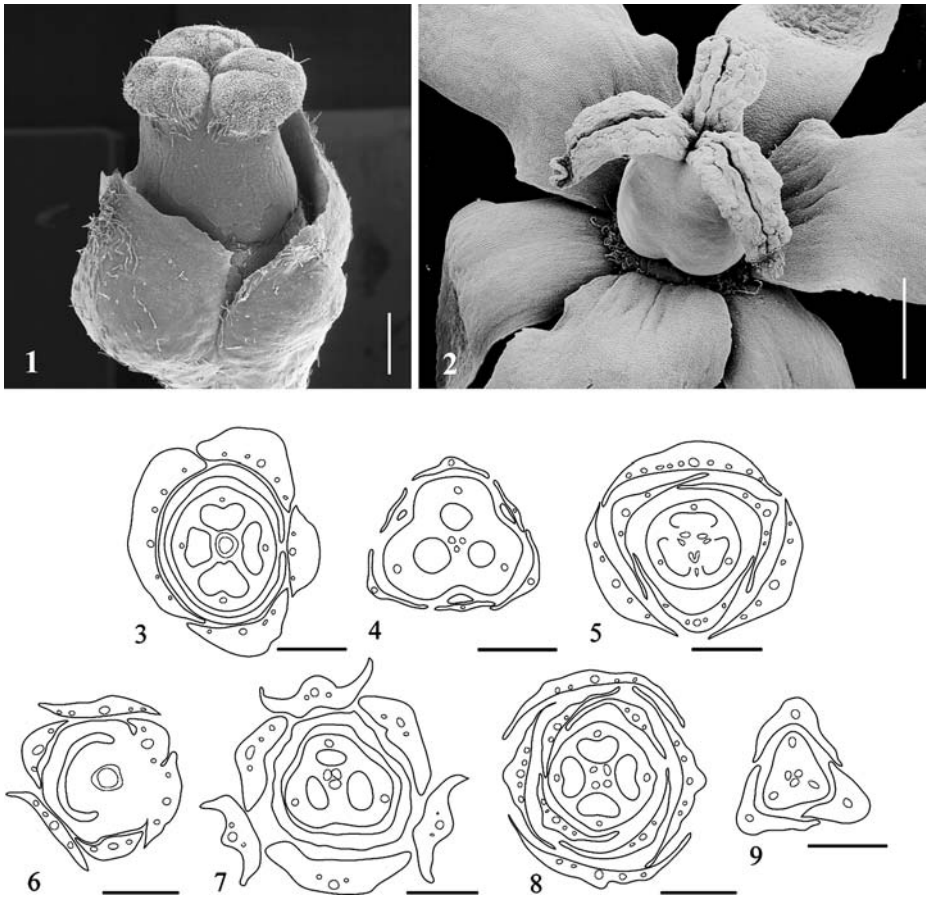
Nucellar cap (histological term)**:** A plurilayered tissue at the nucellus apex derived from periclinal divisions of epidermal cells (Bouman 1984, Johri et al. 1992) or of epidermal and/or hypodermal cells (Maheshwari 1950, Kapil and Bhatnagar 1994). These two variants cannot always be easily distinguished.

Nucellar beak (morphological term)**:** The elongate apical part of a nucellus, which protrudes into or through the micropyle (Bouman 1984, Johri et al. 1992, Kapil and Bhatnagar 1994), at the histological level commonly concomitant with a nucellar cap.

Nucellar pad: A strand of especially differentiated tissue formed below the nucellar apex by radially elongate cell files in the nucellar epidermis and hypodermal area, which apparently forms the pathway for pollen tubes from the nucellus apex to the embryo sac (Johri et al. 1992).

Secondary septum: A complete or incomplete wall subdividing each locule of the ovary between the two ovules.

Obturator size: Is defined here in relation to ovule size (volume).



Figs. 1–2. SEM micrographs of female flowers at anthesis. **1** *Austrobuxus megacarpus* (B.H. 13521). **2** *Micrantheum hexandrum* (Scale bars = 1 mm). **Figs. 3–9** TS of female flowers, showing perianth aestivation. **3** *Austrobuxus megacarpus* (PIF 19209), imbricate. **4** *Choriceras majus,* open. **5** *Dissiliaria baloghioides,* imbricate. **6** *Dissiliaria muelleri*, open. **7** *Micrantheum hexandrum*, open. **8** *Petalostigma pubescens*, imbricate. **9** *Sankowskya stipularis*, imbricate. (Scale bars = 1 mm)

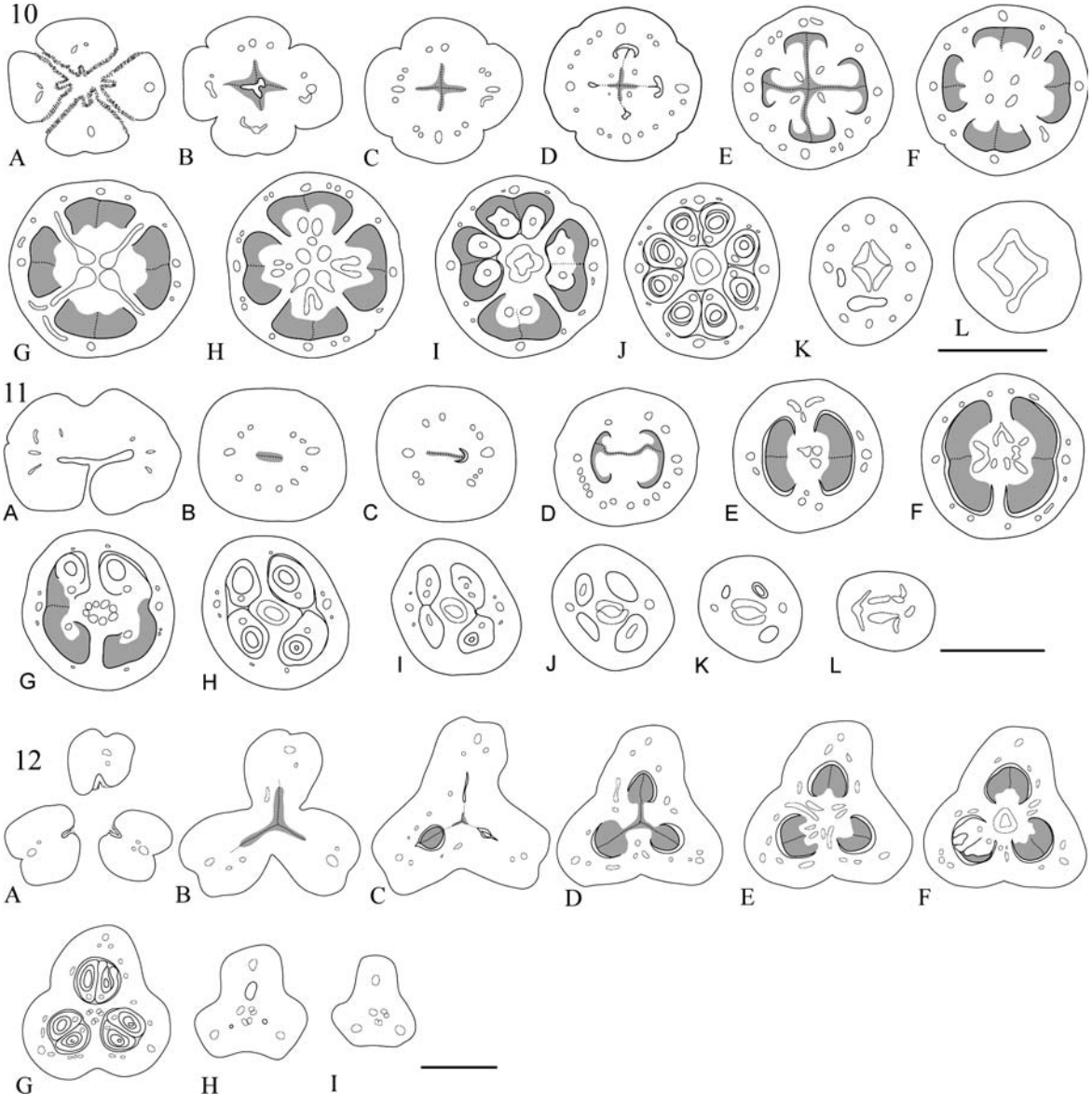
PTTT: Abbreviation for ''Pollen tube transmitting tract'', the pathway for pollen tubes within the gynoecium.

Epitropous (antitropous): related to the curvature direction of the anatropous ovule, which is opposite to the curvature direction of the carpel (Endress 1994).

Results

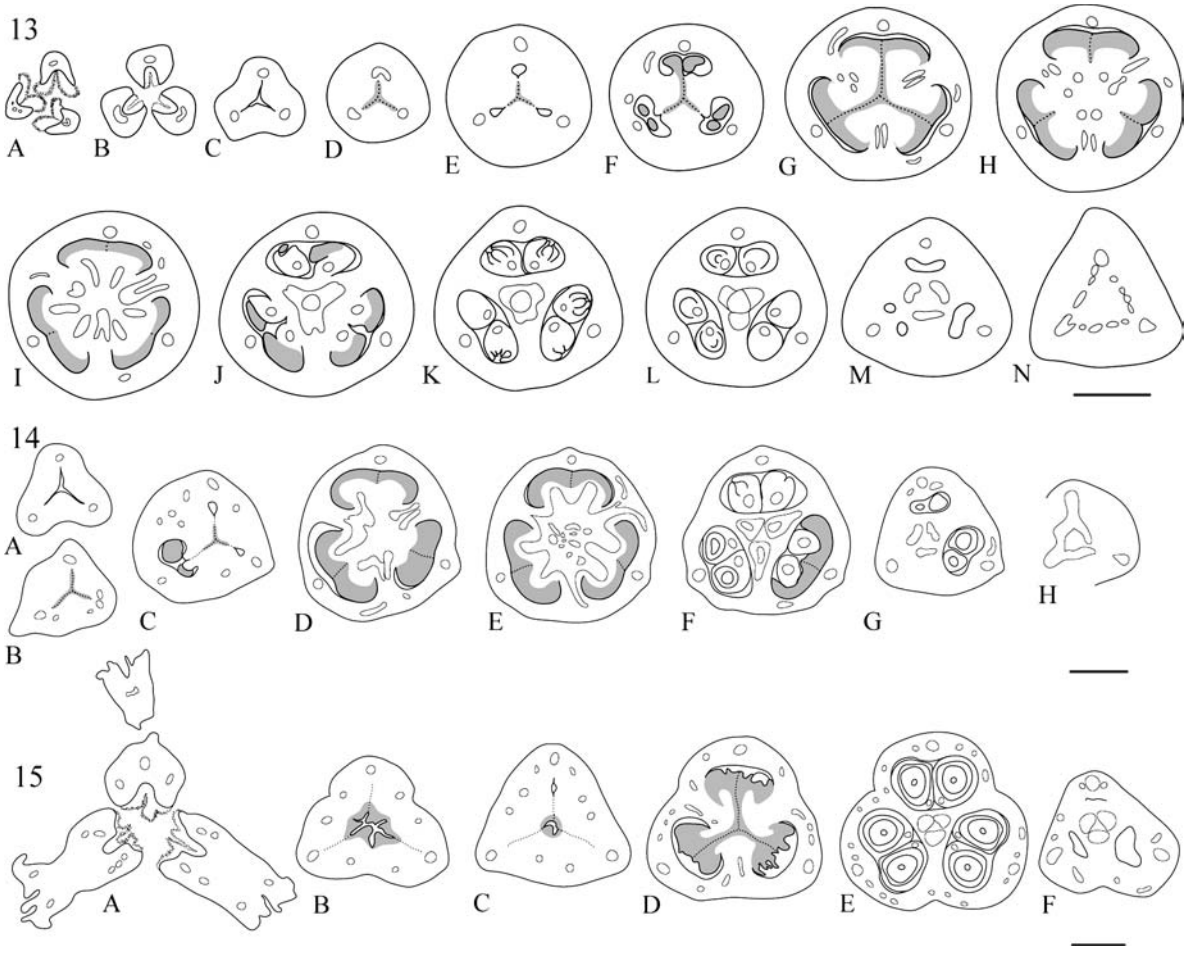
The descriptions are for anthetic flowers.

Austrobuxus megacarpus. Flowers have a single perianth whorl of four sepals (Fig. 1). Aestivation is imbricate with one inner, one outer and two intermediate sepals (Fig. 3). A nectary disc with uni- or multicellular (uniseriate), unlignified hairs is present. The gynoecium is of angiospermy type 4. The 2–4 carpels are free above the ovary, they are entire (not bifurcate) and have a ventral furrow (Figs. 10, 11). The stigma appears to be dry and is unicellular papillate. The ovary is synascidiate for two thirds of its length. The two ovules per carpel are bitegmic, crassinucellar, anatropous and epitropous. A nucellar cap and pad are present. A nucellar beak may also be present (Fig. 21). The micropyle is formed by the inner integument, and it is slightly open. The micropyle



Figs. 10–12. TS series of gynoecia of anthetic flowers, morphological surfaces drawn with solid line, postgenitally fused areas indicated with dashed lines, PTTT shaded grey. **10** *Austrobuxus megacarpus* (PIF 19209); **A** stigmatic region of the free carpels, plicate zone; **B–E** symplicate zone; **F–K** synascidiate zone; **L** Gynoecium base. **11** *Austrobuxus megacarpus* (B.H. 13521); **A–D** symplicate zone; **E–K** synascidiate zone; **L** Gynoecium base. **12** *Choriceras majus*; **A** stigmatic region of the free carpels, plicate zone; **B–D** symplicate zone; **E–H** synascidiate zone; **I** Gynoecium base. (Scale bars = 1 mm)

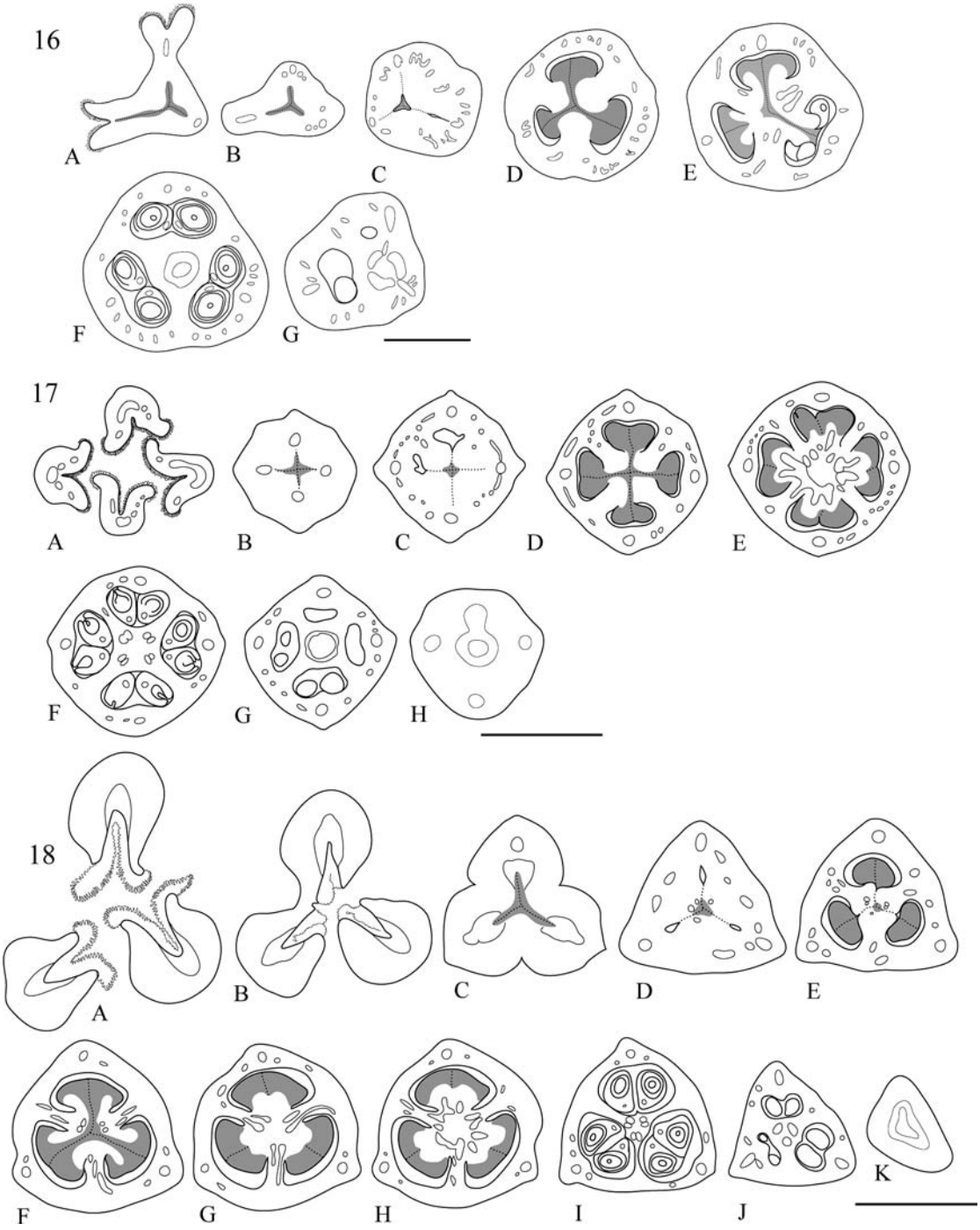
opening is round or slit-like and is filled by the intruding obturator (Figs. 20, 21). The obturator is larger than the ovules (Figs. 19, 33). Few unlignified, unicellular hairs are present at the base of the locule wall (collection PIF 19209). A short secondary septum at the base between the two ovules of a locule reaching only up to a tenth of the locule length was found (collection B.H. 13521).



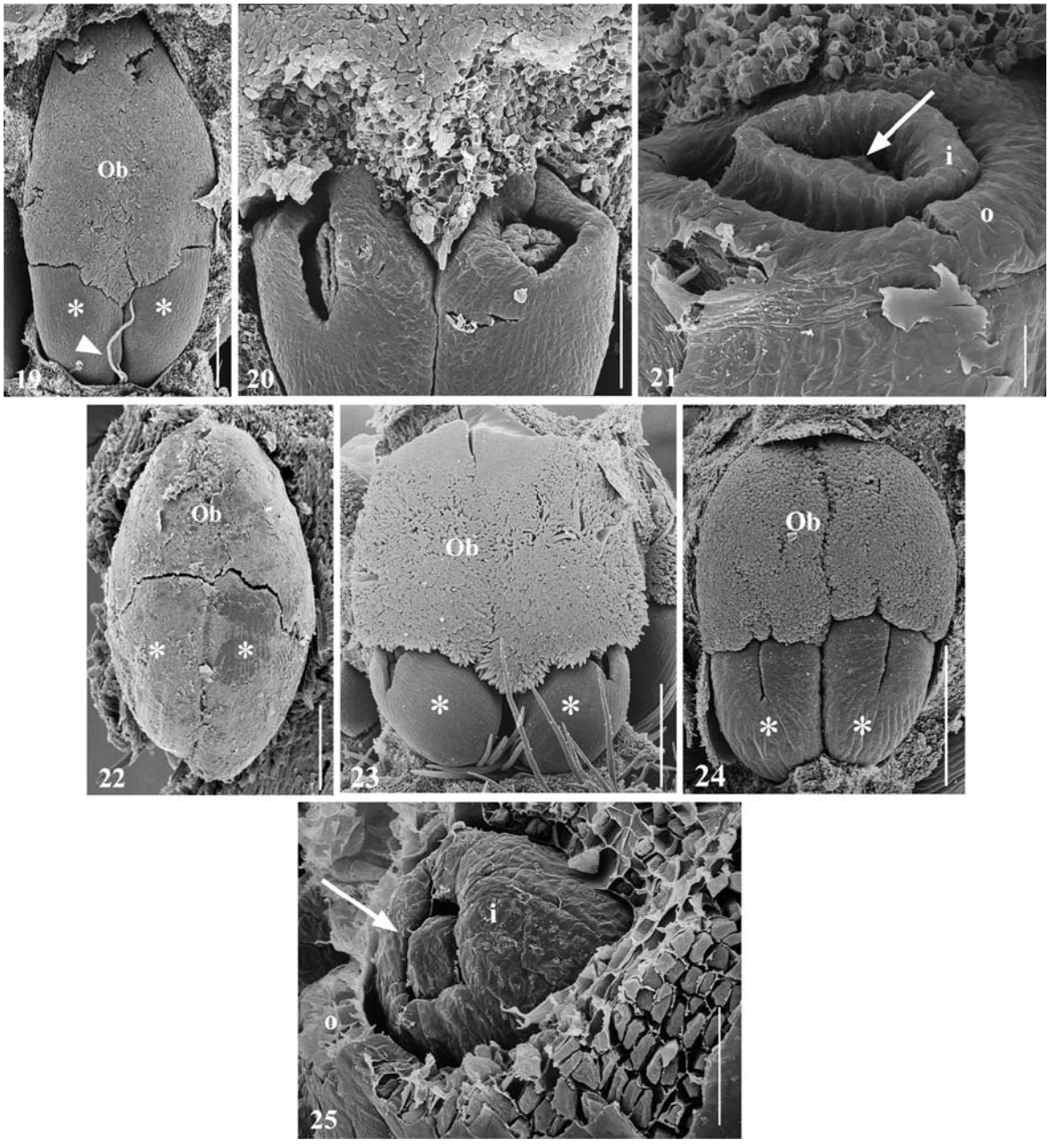
Figs. 13–15. TS series of gynoecia of anthetic flowers, morphological surfaces drawn with solid line, postgenitally fused areas indicated with dashed lines, PTTT shaded grey. **13** *Dissiliaria baloghioides*; **A–B** stigmatic region of the free carpels, plicate zone of carpels; **C–G** symplicate zone; **H–M** synascidiate zone; **N** Gynoecium base. **14** *Dissiliaria muellerii*; **A–D** symplicate zone; **E–G** synascidiate zone; **H** Gynoecium base. **15** *Micrantheum hexandrum*; **A** stigmatic region of the free carpels, plicate zone; **B–D** symplicate zone; **E–F** synascidiate zone. (Scale bars = 0.5 mm)

The carpels have a dorsal vascular bundle which extends up to the stigmatic region (Figs. 10, 11). In the style and upper ovary several smaller lateral bundles are present. They form an irregular network between themselves and with the dorsal bundle. In the upper ovary these lateral bundles unite into synlaterals, which extend downwards into the septa between the locules. In the synascidiate zone, the synlateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle branches in the chalazal region, and the branches end at the base of the inner integument. At the base of the ovary the dorsal bundles join the central vascular complex, and together they form a ring-shaped stele.

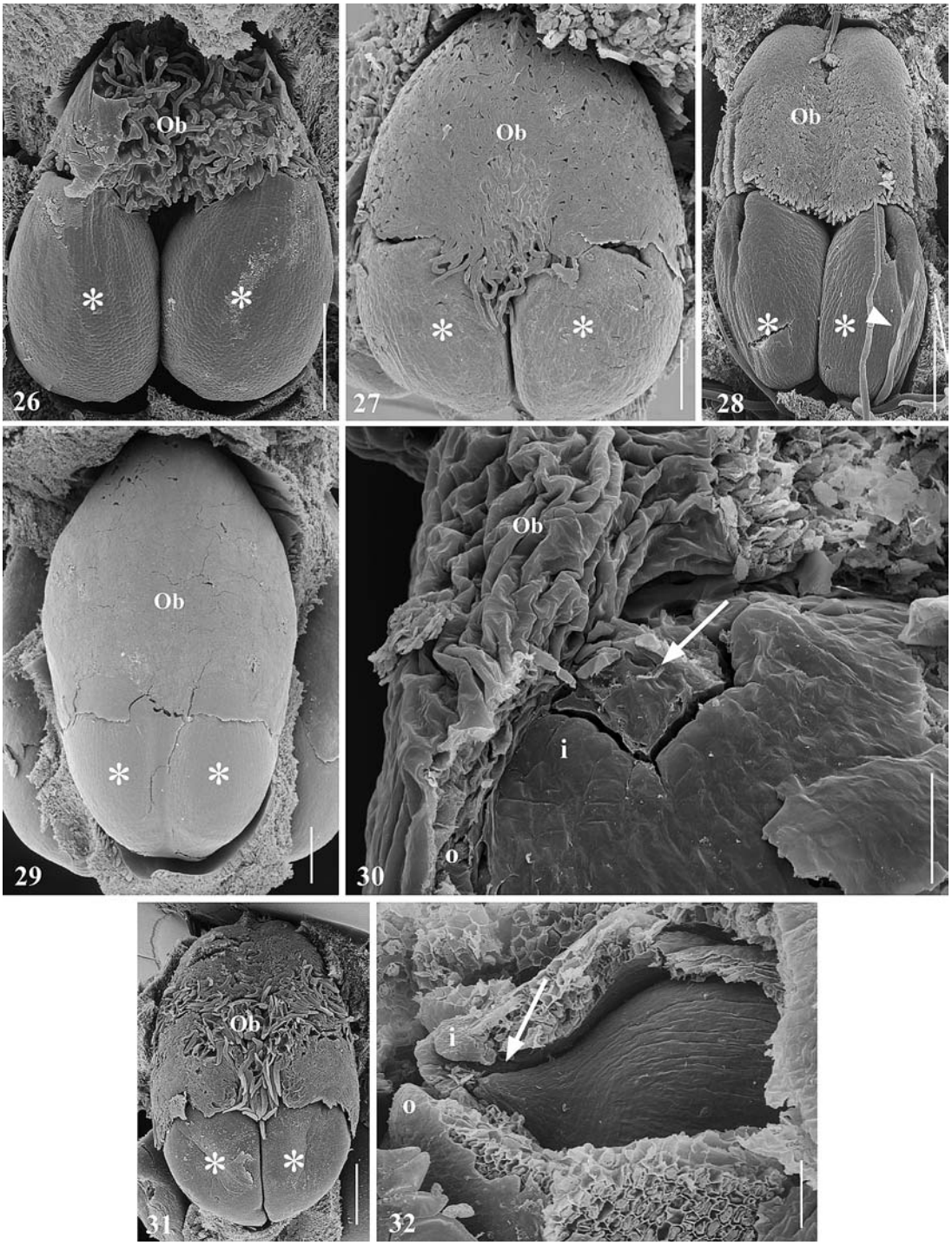
The PTTT is one cell layer thick lining the ventral furrow of the plicate zone. A compitum may be present in the symplicate zone, and at the level of the upper third of the locules it divides into four horizontal branches, each entering a locule via the surface of the obturator. The outer integument is 3 or 4 cell layers



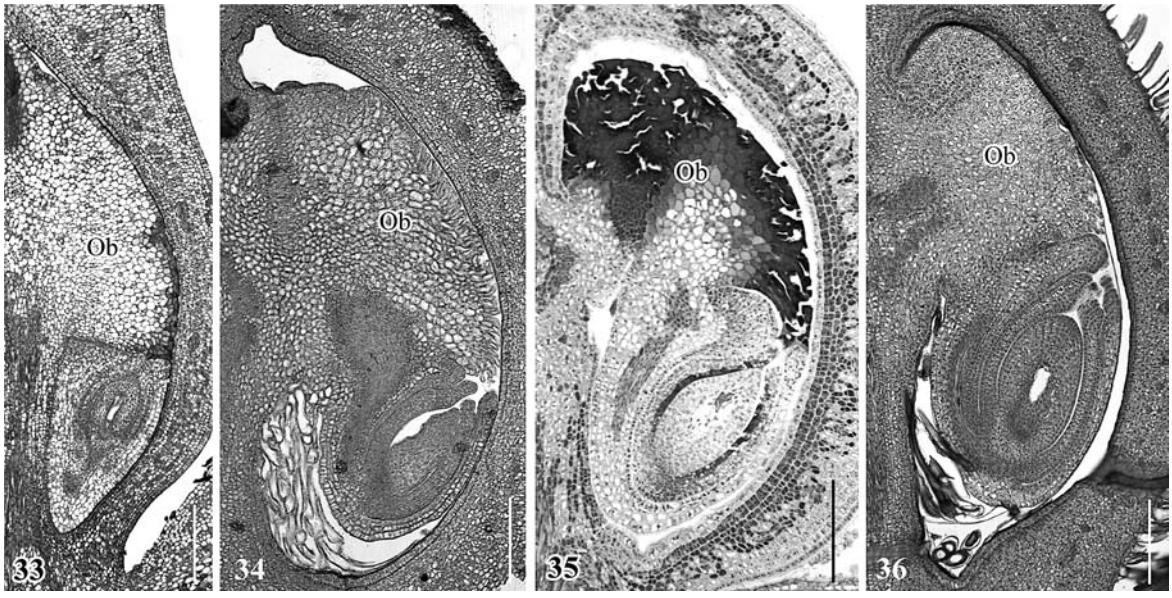
Figs. 16–18. TS series of gynoecia of anthetic flowers, morphological surfaces drawn with solid line, postgenitally fused areas indicated with dashed lines, PTTT shaded grey. **16** *Neoroepera banskii*; **A–E** symplicate zone; **F–G** synascidiate zone. **17** *Petalostigma pubescens*; **A** stigmatic region of the free carpels, plicate zone; **B–D** symplicate zone; **E–G** synascidiate zone; **H** Gynoecium base. **18** *Sankowskya stipularis*; **A** stigmatic region of the free carpels, plicate zone; **B–F** symplicate zone; **G–K** synascidiate zone. (Scale bars = 1 mm)



Figs. 19–25. SEM micrographs of ovules and obturators (*i* inner integument, *o* outer integument, *Ob* obturator, *asterisk* ovule). **19–21** *Austrobuxus megacarpus* (19, 20, PIF 19209; 21, B.H. 13521). **19** Ovules with obturator and few intraovarian hairs (arrow head). **20** Slit-like and round micropyle (obturator partly removed) exostome open, endostome closed. **21** Open micropyle with tip of the nucellar beak (arrow). **22** *Choriceras majus*, ovules with obturator. **23** *Dissiliaria baloghioides*, ovules with obturator and intraovarian hairs. **24–25** *Dissiliaria muellerii*. **24** Ovules with slit-like micropyle and obturator. **25** Micropyle (uppermost part of outer integument removed), endostome open with nucellar beak (arrow). (Scale bars: 19, 22–24 = 0.3 mm; 20 = 0.2 mm; 21, 25 = 50 μm)



Figs. 26–32. SEM micrographs of ovules and obturators (*i* inner integument, *o* outer integument, *Ob* obturator, *asterisk* ovule). **26** *Micrantheum hexandrum*, ovules with obturator. **27** *Neoroepera banskii*, ovules with obturator. **28** *Petalostigma pubescens*, ovules with obturator and intraovarian hairs (arrow head). **29, 30** *Sankowskya stipularis*. **29** Ovules with obturator. **30** Micropyle (uppermost part of outer integument and obturator partly removed), endostome open with nucellar beak (arrow). **31, 32** *Whyanbeelia terrae-reginae*. **31** Ovules with obturator. **32** Micropyle (integuments partly removed on one side), showing nucellus with pointed nucellus (arrow). (Scale bars: 26–29 = 0.2 mm; 30, 32 = 50 μm; 31 = 0.3 mm)



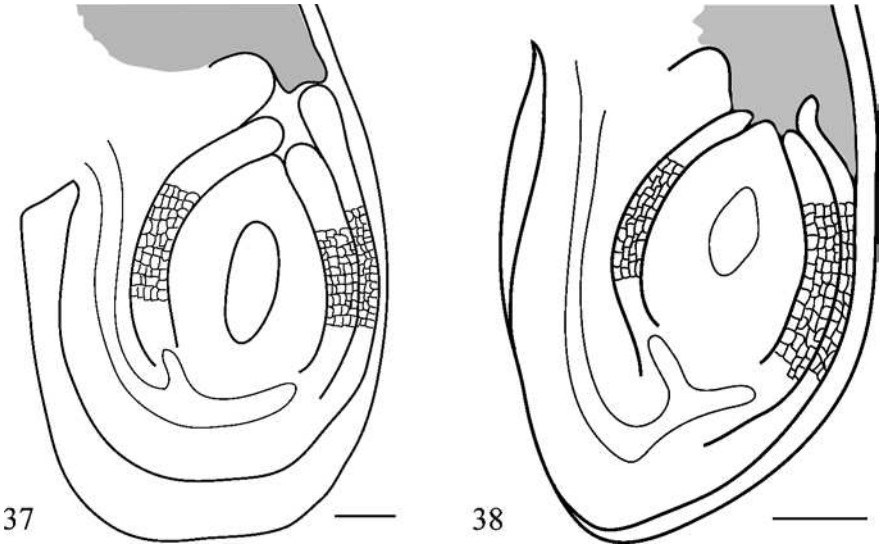
Figs. 33–36. Longitudinal sections of ovules and obturators, placenta on the left (*Ob* obturator). **33** *Austrobuxus megacarpus* (B.H.13521). **34** *Dissiliaria baloghioides*. **35** *Neoroepera banskii*. **36** *Petalostigma pubescens*. (Scale bars: 33 = 0.3 mm; 34–36 = 0.2 mm)

thick, the inner 4 cell layers. The rims of the outer integument may be thickened. There is a space between the outer and inner integument. Tanniferous tissue is not present. Cells containing oxalate druses and cells with a thickened, mucilaginous inner wall are present in the mesophyll of sepals and gynoecium (plicate and uppermost symplicate zone).

Choriceras majus. Flowers are 3-merous with two perianth whorls of sepals. Aestivation in each whorl is open but the sepals overlap between whorls (Fig. 4). The nectary disc segments are glabrous. The gynoecium is of angiospermy type 4. The carpels are free above the ovary and entire with a ventral furrow (Fig. 12). The stigma appears dry and is unicellular papillate. The ovary is synascidate for half of its length. The two ovules per locule are bitegmic, crassinucellar, anatropous and epitropous. The micropyle is formed by both integuments, the exostome is open forming a triangle-shaped opening and is filled by the intruding obturator. A nucellar cap or beak are absent. The obturator is as large as the ovules (Fig. 22). Few unlignified unicellular hairs are present in the locule, originating on the ventral side of the wall.

Carpels have a dorsal vascular bundle, which extends up to the stigmatic region (Fig. 12). In the style and upper ovary several smaller lateral bundles are present. They form an irregular network between themselves and the dorsal bundle. In the upper ovary the lateral bundles extend downwards into the septa between the locules. In the synascidiate zone the lateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle branches in the chalazal region and the branches end at the base of the inner integument. At the base of the ovary the dorsal bundles join the central vascular complex and form a ring-shaped stele.

The PTTT is one cell layer thick in the ventral furrow of the plicate and uppermost symplicate zone. The compitum divides into three horizontal branches in the upper half of the locule, each entering a locule via the surface of the obturator. Both integuments are 4 cell layers thick. The rim of the outer integument is thickened. The inner epidermis



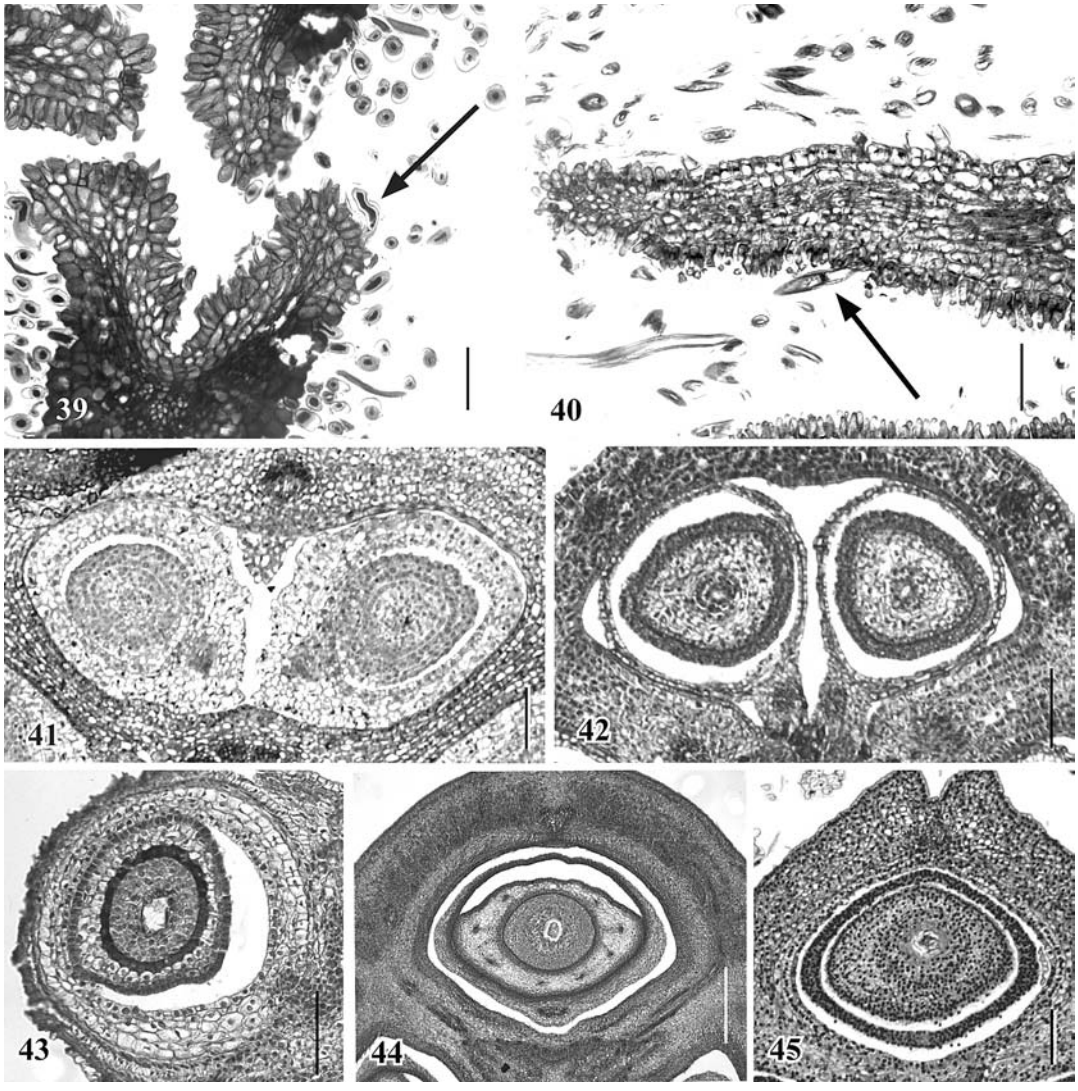
Figs. 37–38. Median longitudinal sections of ovules. **37** *Sankowskya stipularis*. **38** *Micrantheum hexandrum*. (Scale bars = 0.1 mm)

of the inner integument is tanniferous. Tanniferous tissue is also present in other parts of the ovary. Cells containing oxalate crystals or druses are absent.

Dissiliaria baloghioides and D. muelleri. Flowers are mainly 3-merous with two perianth whorls of sepals. In *D. baloghioides* aestivation is imbricate in each whorl with one inner, one outer and one intermediate sepal (Fig. 5). In *D. muelleri* aestivation in each whorl is open but the sepals between whorls overlap (Fig. 6). A nectary disc with uni- or multicellular (uniseriate), unlignified hairs is present. The gynoecium is of angiospermy type 4. The three (three or four in *D. muelleri*) carpels are free above the ovary, they are entire and have a ventral furrow (Figs. 13, 14). The stigma appears dry and is unicellular papillate with long uni- or multicellular hairs interspersed between the papillate cells (Fig. 39). The ovary is synascidiate for two thirds of its length. The two ovules per carpel are bitegmic, crassinucellar, hemitropous and epitropous. A nucellar cap and pad are present. In *D. muelleri* a nucellar beak is present (Fig. 25). The micropyle is formed by both integuments. The obturator is larger than the ovules and covers part of the micropyle but does not intrude (Figs. 23, 24, 34). In *D. baloghioides* the exostome and endostome are slightly open (Fig. 34), the opening being triangle-shaped. In *D. muelleri* only the endostome is open and the micropyle is slit-like. Unlignified, unicellular hairs are present on the ventral side of the locule wall (Fig. 34).

Carpels have a dorsal vascular bundle, which extends up to the stigmatic region (Figs. 13, 14). In the upper ovary several smaller lateral bundles are present, they form an irregular network between themselves and with the dorsal bundle. Lower down they unite into synlaterals, which extend downwards into the septa between the locules. In the synascidiate part, the synlateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle ends at the base of the nucellus (*D. baloghioides*) or branches in the chalazal region and the three branches end at the base of the inner integument (*D. muelleri*). At the base of the ovary the dorsal bundles join the central vascular complex, and together they form a ring-shaped stele.

The PTTT is one cell layer thick lining the ventral furrow of the plicate zone. A central gap between the carpels is present in the



Figs. 39–45. TS stigmatic region, with hairs interspersed between the unicellular stigmatic papillae (arrows). **39** *Dissiliaria baloghioides*. **40** *Petalostigma pubescens*. **Figs. 41–45** TS ovary locule with ovules, showing spaces between integuments and/or inner integument and nucellus. **41** *Austrobuxus megacarpus* (PIF 19209) (Picrodendraceae). **42** *Andrachne colchica* Boiss. (Phyllanthaceae) (Sutter 36, cult. Botanic Garden, University of Zurich). **43** *Acalypha hispida* Willd. (Euphorbiaceae-Acalyphoideae) (Sutter 5/22, cult. Botanic Garden, University of Zurich). **44** *Manihot esculenta* Crantz (Euphorbiaceae-Crotonoideae) (Sutter 28/31, cult. Botanic Garden, University of Zurich). **45** *Monadenium guentheri* Pax (Euphorbiaceae-Euphorbioideae) (Sutter 30/40, cult. Botanic Garden, University of Zurich). (Scale bars: 39, 40 = 50 μm; 41–43, 45 = 0.1 mm; 44 = 0.3 mm)

uppermost symplicate zone lined by a single layer of PTTT. A compitum may be present in the symplicate zone below the central gap; in the upper third of the locules the compitum divides into three horizontal branches, each entering a locule via the surface of the obturator. The outer integument is 3 cell layers thick, the inner integument is 4 (3 or 4 in *D. muelleri*) cell layers thick. The rims of the outer integument may be thickened. There is a space between the outer and inner integument. Tanniferous tissue is not present. Few cells containing oxalate crystals and druses are present in the sepals, ovary wall and style.

Micrantheum hexandrum. Flowers are 3-merous with two perianth whorls of sepals (Fig. 2) (see also Berg 1975). Aestivation in each whorl is open, but the sepals overlap between whorls (Fig. 7). The nectary disc is glabrous. The gynoecium is of angiospermy type 4. The carpels are free above the ovary and are entire with a ventral furrow (Fig. 15). The stigma is unicellular papillate (see also Berg 1975) and appears wet. The ovary is synascidiate for half of its length. The two ovules per carpel are bitegmic, crassinucellar, anatropous and epitropous. A nucellar cap and pad are present (see also Berg 1975). The micropyle is formed by both integuments, the exostome is open, round and filled by the intruding obturator (Fig. 37) (see also Berg 1975). The obturator is smaller than the ovules (Fig. 26). There are no intraovarian hairs.

Carpels have a dorsal and two lateral vascular bundles, which extend up to the stigmatic region (Fig. 15). In the style and upper ovary several smaller lateral bundles are present. They form an irregular network between themselves and the dorsal bundle. In the upper ovary the lateral bundles extend downwards into the septa between the locules. In the synascidiate zone the lateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle branches in the chalazal region and the branches end at the base of the inner integument (Fig. 37). At the base of the ovary the dorsal bundles join the central vascular complex and form a ring-shaped stele.

The PTTT is 1–3 cell layers thick lining the ventral furrow of the plicate zone. A compitum appears to be present in the symplicate zone, it is 3 or 4 cell layers thick in the upper half and 1–3 cell layers thick in the lower half of the symplicate zone. At the level of the upper half of the locules the compitum divides into three horizontal branches, each entering a locule via the surface of the obturator. The outer integument is 3 or 4 cell layers thick, the inner 5 cell layers (Fig. 37) (see also Berg 1975). The rim of the outer integument is thickened. The outer epidermis of the outer integument consists of radially enlarged cells (see also Berg 1975). The inner epidermis of the inner integument is tanniferous. Tanniferous tissue is also present in the sepals, compitum and obturator surface. Cells containing oxalate druses are present in the sepals (few), carpel wall and style (few).

Neoroepera banksii. Flowers are 3-merous with two perianth whorls of sepals. Aestivation is open (but imbricate in flower buds). The nectary disc segments are glabrous. The gynoecium is of angiospermy type 4. The carpels are free above the ovary and are entire with a ventral furrow (Fig. 16). The stigma is unicellular papillate. The ovary is synascidiate for half of its length. The two ovules per locule are bitegmic, crassinucellar, anatropous and epitropous. The micropyle is formed by both integuments and is slightly open, with a round opening, which is filled by the intruding obturator. A nucellar beak is absent, and a cap also appears to be absent. An inconspicuous nucellar pad may be present. The obturator is as large as the ovules (Figs. 27, 35).

Carpels have a dorsal vascular bundle, which extends up to the stigmatic region (Fig. 16). In the style and upper ovary several smaller lateral bundles are present. They form an irregular network between themselves and the dorsal bundle. In the upper ovary the lateral bundles extend downwards into the septa between the locules. In the synascidiate zone the lateral bundles and the two ovular bundles from each carpel unite into a central vascular complex. The ovular bundle branches in the chalazal region and the branches end at the base of the inner integument. At the base of the ovary the dorsal bundles join the central vascular complex and form a ring-shaped stele.

The PTTT is 1–3 cell layers thick in the ventral furrow of the plicate zone and about 3 cell layers thick in the uppermost symplicate zone. A compitum also comprising about 3 cell layers may be present in the symplicate part. At the level of the upper half of the locule the compitum divides into three horizontal branches each entering a locule via the surface of the obturator. The outer integument is 3 cell layers thick, the inner 4 cell layers. The rim of

the outer integument is thickened. The inner epidermis of the inner integument is tanniferous (Fig. 35). Tanniferous tissue is also present in the sepals, stigma, PTTT and obturator surface (Fig. 35). Cells containing oxalate druses are present in the sepals, carpel wall and style (few).

Petalostigma pubescens. Flowers are 4-merous with two perianth whorls of sepals. Aestivation is imbricate in each whorl (Fig. 8). The outer whorl has two outer and two inner sepals, the inner whorl is contort. The gynoecium is of angiospermy type 4. The carpels are free above the ovary and are entire with a ventral furrow (Fig. 17). The stigma appears dry, it is unicellular papillate and with long unicellular or multicellular hairs interspersed between the papillate cells (in accordance with the results of Forster and Van Welzen 1999) (Fig. 40). The ovary is synascidiate for two thirds of its length. The two ovules per locule are bitegmic, crassinucellar, hemitropous and epitropous. A nucellar cap and pad are present. The micropyle is formed by both integuments and is open and slit-like. The obturator reaches only into the upper end of the micropyle. It is as large as the ovules (Figs. 28, 36). Unlignified, unicellular hairs originate on the ventral side of the locule wall; they leave indents on the ovules and obturator (Fig. 36).

Carpels have a dorsal vascular bundle, which extends up to the stigmatic region (Fig. 17). In the upper ovary several smaller lateral bundles are present. The lateral bundles form an irregular network between themselves and the dorsal bundle. They unite into synlaterals, which extend downwards into the septa between the locules. In the synascidiate zone, the synlateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle branches in the chalaza and the branches end at the base of the inner integument. There are no vascular bundles in the integuments. At the base of the ovary the dorsal bundles join the central vascular complex, and together form a ring-shaped stele.

The PTTT is one cell layer thick lining the ventral furrow of the plicate zone. A central gap between the carpels is present in the uppermost symplicate part lined by a single layer of PTTT. A compitum may be present in the symplicate part below the central gap. At the level of the upper third of the locule the compitum divides into four horizontal branches each entering a locule via the surface of the obturator. The outer integument is 3 or 4 cell layers thick, the inner 4 cell layers. The integuments are free from each other. The rim of the outer integument may be thickened. The inner and outer epidermis of the inner integument are stained darker than the hypodermal cells of the inner integument but are not obviously tanniferous. Tanniferous tissue is present in the sepals. Cells containing oxalate druses are present in the sepals (adaxial hypodermis), ovary wall and style.

Sankowskya stipularis. Flowers are 3-merous with one perianth whorl of sepals (see also Forster 1995). Aestivation is imbricate with one inner, one outer and one intermediate sepal (Fig. 9). Nectary disc segments are without hairs. The gynoecium is of angiospermy type 4. The carpels are free above the ovary, they are entire with a ventral furrow (Fig. 18). The stigma appears wet, it is unicellular papillate with long hairs interspersed between the papillate cells. The ovary is synascidiate for two thirds of its length. The two ovules per locule are bitegmic, crassinucellar, anatropous and epitropous. A nucellar beak is present (Figs. 30, 38). The micropyle is formed by both integuments and is open, forming a round opening, which is filled by the intruding obturator. The obturator is larger than the ovules (Fig. 29). There are no intraovarian hairs.

Carpels have a dorsal vascular bundle, which extends up to the stigmatic region (Fig. 18). In the style and upper ovary several smaller lateral bundles are present. They form an irregular network between themselves and with the dorsal bundle. In the upper ovary the laterals extend downwards into the septa between the locules. In the synascidiate zone

the lateral bundles and the two ovular bundles of each carpel unite into a central vascular complex. The ovular bundle branches in the chalazal region and the branches end at the base of the inner integument (Fig. 38). At the base of the ovary the dorsal bundles join the central vascular complex, and together they form a ring-shaped stele.

The PTTT is 4–6 cell layers thick lining the ventral furrow of the plicate zone and in the uppermost symplicate zone. Below, a compitum may be present. At the level of the upper third of the locule the compitum divides into three horizontal branches (c. 4 cell layers thick) each entering a locule via the surface of the obturator. The outer integument is 2 or 3 cell layers thick, the inner integument is 3 or 4 cell layers thick (Fig. 38). The rim of the outer integument is not thickened. Tanniferous tissue is present in the stigma, PTTT and obturator surface. Cells containing oxalate druses are present in the sepals, carpel wall and style.

Whyanbeelia terrae-reginae. The material available was not sufficient to study all the aspects described for the other taxa. Flowers are 3-merous with two perianth whorls of sepals. Aestivation is imbricate (Webster 1994b). Nectary disc segments are glabrous. The gynoecium is of angiospermy type 4. The carpels are free above the ovary, they are entire with a ventral furrow. The stigma is non-papillate, long unicellular or multicellular hairs are interspersed between the stigmatic cells. The ovary is synascidiate for two thirds of its length. The two ovules per locule are bitegmic, probably crassinucellar, anatropous and epitropous. The micropyle is formed by both integuments. The nucellus is pointed but does not form a beak (Fig. 32). The obturator is as large as the ovules (Fig. 31).

A compitum may be present in the symplicate zone. At the level of the upper third of the locule the compitum divides into three horizontal branches each entering a locule via the surface of the obturator. Tanniferous tissue is not present. Few cells containing oxalate crystals and druses are present in the style.

Discussion

Female floral structure of Picrodendraceae

Floral merism, perianth, nectary. The perianth is mainly 3-merous with two whorls (rarely one whorl) of sepals, less often 4-merous with one or two whorls of sepals or more diverse (3–9 (−13)-merous) (Radcliffe-Smith 2001, this study). Petals are absent.

The gynoecium is 3-merous in 17 genera, 2-merous in two genera, and more variable (2–3-, 3–4-, or 3–5-merous in eight genera (Radcliffe-Smith 2001, this study). Where the gynoecium is 3-merous, the perianth is commonly 3-merous with one or two whorls of sepals, or less often more variable (4- to 9-merous) (Radcliffe-Smith 2001). Where the gynoecium is not regularly 3-merous (2–5-merous), sepal number also tends to be unstable (3–13 sepals). Regularly 5-merous taxa do not seem to be present (Radcliffe-Smith 2001).

Sepal aestivation in the species studied is (considering each whorl separately if two are present) often imbricate (in 4- and 3-merous flowers with one or two whorls of sepals) or less often open (in 3-merous flowers with two whorls of sepals). Imbricate aestivation is formed by one inner, one outer and one/two intermediate sepals or by two inner and two outer sepals.

A nectary in the shape of a disc or disc segments (around the base of the gynoecium) is present in all species studied, except for *Petalostigma pubescens*. In other Picrodendraceae a nectary disc is more or less equally often present or absent (Webster 1994b). In three species (*Austrobuxus megacarpus*, *Dissiliaria baloghioides*, *D. muelleri*) uni- or multicellular (uniseriate), unlignified hairs are present on the disc. Hairs on the disc were also reported for *Podocalyx* (Webster 1994b).

Gynoecium. In the taxa investigated (and in most other Picrodendraceae), carpels are free above the ovary, or shortly connate in *Dissiliaria*, *Micrantheum*, and *Whyanbeelia*. The stylar branches are entire; however, in *Croizatia*, *Piranhea*, and *Oldfieldia* they are bifurcate (Radcliffe-Smith 2001). In all taxa

investigated the gynoecium is of angiospermy type 4 (for term, see Glossary and Endress and Igersheim 2000). The ovary is synascidiate for half or two thirds of its length, and symplicate above.

The stigma is unicellular papillate (non-papillate in *Whyanbeelia*) and appears dry in most species (wet in *Sankowskya* and *Micrantheum*). Uni- or multicellular unlignified long hairs are interspersed between the stigmatic cells in varying amounts in *Dissiliaria*, *Sankowskia*, *Whyanbeelia*, and *Petalostigma*.

A ventral furrow is present in the free part of the carpels. It is commonly lined by one cell layer of PTTT, but one to three cell layers in *Neoroepera* and *Micrantheum*, and four to six in *Sankowskya*. In the uppermost symplicate zone of the gynoecium there is a central gap between the carpels, which is lined with PTTT (*Austrobuxus*, *Dissiliaria*, *Petalostigma*). A compitum appears to be present in the symplicate zone in all species. In the upper third or half of the ovary the compitum divides into three or four horizontal branches, each entering a locule via the surface of the obturator. An incomplete secondary septum in the basal part of the locule may be present in *Austrobuxus*. This feature appears to be new for Picrodendraceae.

The carpels always have a dorsal vascular bundle, which extends up to the stigmatic region, and several smaller lateral bundles in the style and upper ovary, which may be united into synlateral bundles. Synlateral bundles are restricted to the synascidiate part, but in *Micrantheum* they are lacking.

Cells containing oxalate crystals or, more often, druses are found in all species studied and occur in the sepals, ovary wall and style. Only in *Choriceras* were crystals and druses absent. In *Austrobuxus*, in the sepals and style distinctive hypodermal (never epidermal) groups of cells with a thickened, mucilaginous inner cell wall are present. The only literature records of similiar mucilage cells in floral parts of rosids in the sepal and carpel epidermis (rarely hypodermis) are by Matthews et al. 2001 and Matthews and Endress (2002, 2004, 2005a,b, 2006) for some Crossosomatales, Oxalidales, Cucurbitales, Fabales, Fagales, Rosales, and *Perrottetia* (now placed in malvids, Zhang and Simmons 2006), and, among Malpighiales, some Ochnaceae, Rhizophoraceae, and Violaceae. Tanniferous tissue is present in various areas of the floral organs in half of the species studied. In *Choriceras* it is found in the ovary, in *Sankowskya*, *Neoroepera* and *Micrantheum* in the stigma, PTTT, compitum and obturator surface, and in *Petalostigma* only in the sepals. Intra-ovarian hairs are present in five of the ten species here investigated and also in *Picrodendron baccatum* (Hakki 1985). They originate on the ventral side or at the base of the locule and are unicellular, unlignified, and non-secretory.

Ovules. All species studied have two ovules per carpel. They are bitegmic, crassinucellar (and relatively thick in the range of crassinucellar ovules), anatropous or hemitropous, and epitropous. The two integuments and the nucellus tend to be separated from each other by a narrow space, as seen in *Austrobuxus, Dissiliaria,* and *Petalostigma*. An obturator is always present and is as large as or larger than the ovules (see also Berg 1975, Hayden et al. 1984, Hakki 1985, Radcliffe-Smith 2001). Sometimes the obturator intrudes into the micropyle to various degrees, which may lead to different shapes of the micropyle: it is circular, slit-like or triangular. However, there are also micropyles that are open without an intruding obturator (*Dissiliaria baloghioides*, *Petalostigma*). The micropyle is commonly formed by both integuments but only by the inner integument in *Austrobuxus*. The rim of either both or only the outer (sometimes none) integument(s) is more or less thickened. Seeds commonly have caruncles (Levin and Simpson 1994), which develop from this rim of the outer integument (Berg 1975).

In most species of this study the inner integument is thicker (3–5 cell layers) than the outer (2 or 3 cell layers). Only in *Austrobuxus* and *Choriceras* may the outer integument be as thick as the inner (3 or 4 and 4 cell layers,

respectively) (this study). In *Picrodendron* the outer integument is thicker (5 or 6 cell layers) than the inner (4 cell layers) (Hakki 1985).

Vascular bundles in the integuments are not present. In most species studied the bundle that serves the ovule branches in the chalazal region, and the branches end at the base of the inner integument. More rarely, the vascular bundle ends in the chalaza without branching (*Dissiliaria baloghioides*, this study; *Picrodendron*, Hakki 1985).

In some species the cells of the inner epidermis of the inner integument are tanniferous (or darkly stained but not obviously tanniferous). However, these cells are not radially elongated in the manner of an endothelium.

In the ovules of Picrodendraceae studied here, the nucellar apex shows three kinds of differentiations: (1) a nucellar cap is formed (*Austrobuxus*, *Dissiliaria*, *Micrantheum*, *Petalostigma*, *Whyanbeelia*; (2) the nucellar apex turns into a nucellar beak (*Austrobuxus*, *Dissiliaria muelleri*, *Sankowskya*), and (3) a nucellar pad is formed (*Austrobuxus*, *Dissiliaria*, *Petalostigma*, *Micrantheum*, *Neoroepera*). In general, a nucellar beak that protrudes into or through the micropyle is less common than a nucellar cap. The presence of a nucellar pad is not correlated with a nucellar cap or beak. Also, there is no correlation between the number of cell layers in the nucellar apex in nucelli with or without a pad.

Female floral structure of Picrodendraceae compared with other Euphorbiaceae s.l.

In Picrodendraceae and all other Euphorbiaceae s.l. flowers are unisexual (Webster 1994b), and trimerous female flowers are common. However, compared with Picrodendraceae (with prevailing 3-mery in perianth and gynoecium), merism in the other Euphorbiaceae s.l. is more variable. In Phyllanthaceae, the perianth is 5-merous in 4 (out of 7) tribes, it is more variable with a fluctuation between 3–9-merous in 3 tribes. Petals are present (and then 5) equally as often as they are absent. The gynoecium is 3-merous in 3 tribes, 2-merous in 1 tribe, and more variable with a fluctuation between 2–3- or 3–5-merous in 3 tribes. Where the gynoecium is 3-merous, the perianth is 5-merous. Where the gynoecium is more variable, the perianth is also variable. In Pandaceae the perianth is 5 merous (petals present), and the gynoecium is 2–5 merous (variable in each genus). In Putranjivaceae the perianth is 4- or 5- merous (petals absent), and the gynoecium is 1-, 2-merous (3 genera) or 3-merous (1 genus). In Euphorbiaceae s.str., the perianth is 5-merous in 11 (out of 37) tribes, and 3-merous in 1 tribe), more variable (3–8-merous) in 26 tribes. Petals are more often absent (24 tribes) than present (13 tribes) (and then 5). The gynoecium is 3-merous in 24 tribes, but variably 2–6-merous (fluctuating within the genera) in 13 tribes.

Floral discs (nectaries) are present or absent in all families but Pandaceae (Webster 1994b). In some Euphorbiaceae s.str. (*Euphorbia*; Meeuse et al. 1989) without floral nectaries, extrafloral nectaries are instrumental in pollination biology instead. Hairs on the floral nectary, as found in Picrodendraceae, are also mentioned in Euphorbiaceae s.str. for ten genera (Webster 1994b). However, they are not recorded for Phyllanthaceae, Pandaceae or Putranjivaceae (Webster 1994b).

Bifid stigmas are present in all families to various degrees. Whereas in Picrodendraceae they are rare, they are most common in Phyllanthaceae. In Pandaceae they are bifid to multifid. In Putranjivaceae they are entire (3 genera) or bifid (1 genus). In Euphorbiaceae s.str. the stylar shape varies in each subfamily: in Acalyphoideae entire to bifid or multifid, in Crotonoideae bifid to multifid, rarely entire, and in Euphorbioideae commonly entire, less often bifid (Endress 1994, Webster 1994b).

A secondary septum between the two ovules of each carpel was found in one genus of Picrodendraceae (*Austrobuxus*, this study) and in one genus (*Martretia*) of Phyllanthaceae (Radcliffe-Smith 2001). In the other three families, the carpels are uniovulate, and thus, secondary septa are not formed.

The ovules are bitegmic and crassinucellar in all five families. They are epitropous (except for Pandaceae: in *Microdesmis* intermediate between epitropous and apotropous, pers. obs.) and commonly anatropous (but sometimes hemitropous in Picrodendraceae and Phyllanthaceae), and in Pandaceae hemitropous (*Microdesmis*, pers. obs.), anatropous (and possibly orthotropous) (*Galearia*, Forman 1966, 1972), or orthotropous (*Panda*, Forman 1966). In all families, exept Pandaceae, an obturator is always present (Radcliffe-Smith 2001, this study), which often intrudes into the micropyle. As in Picrodendraceae, in Phyllanthaceae, Putranjivaceae and Euphorbiaceae s. str. the obturator is often as large as or even larger (in volume) than the ovules.

The presence of a gap between the integuments and between inner integument and nucellus as found here in Picrodendraceae (Fig. 41) seems to be common also in Phyllanthaceae and Euphorbiaceeae s.str. (Figs. 42–45) (e.g. Kapil 1961, Chopra 1970, Venkateswarlu and Rao 1975, Bor and Kapil 1976, Sutter and Endress 1995).

The micropyle is commonly formed by both integuments in Euphorbiaceae s.str., and mostly in Picrodendraceae, Phyllanthaceae, and Putranjivaceae (Sutter and Endress 1995; Tokuoka and Tobe 1998, 1999, 2001, 2002, 2003). In Pandaceae the micropyle is formed by the inner integument (pers. observ.), and rarely also in the other four families.

The inner integument is commonly thicker than the outer in the mature ovule, not only in Picrodendraceae, but also in other Euphorbiaceae s.l. In Phyllanthaceae the inner integument is thicker, as thick as, or thinner than the outer integument (outer 2–5, inner 2 or 3 cell layers) (Mukherjee and Padhye 1964; Singh 1968, 1972, pers. obs.). For Euphorbiaceae s.str, in subfamily Acalyphoideae and Euphorbioideae most genera have a thicker inner integument (more than 8 cell layers), the outer only 3–6 cell layers thick (Tokuoka and Tobe 2002, 2003); the same is true for subfamily Crotonoideae (outer 3–8, inner 3–>15 cell layers) (Rao 1964, 1976; Singh 1970a; Bor and Bouman 1974; Rao and Rao 1976, pers. obs.; no data for the outer integument in Tokuoka and Tobe 1998). Also in Putranjivaceae the inner integument is thicker than the outer (outer 3–8, inner 7–14) (Singh 1970b, Tokuoka and Tobe 1999). In Pandaceae (*Microdesmis*) the outer integument is as thick as the inner integument (pers. obs., Tokuoka and Tobe 2003). The presence of an inner integument that is thicker than the outer is a feature of interest at suprafamilial level in Malpighiales and malvids (Endress and Matthews 2006) (see subsequent chapter). In addition, finer patterns of differential integument thickness may be of infrafamilial interest (Tokuoka and Tobe 1995, 2001). Thinnest inner integuments are recorded in Phyllanthaceae (maximally 3 cell layers), followed by Picrodendraceae (3–5), Euphorbiaceae s.str. (more than 8) and Putranjivaceae (7–14).

Vascularisation of mature ovules is diverse in Euphorbiaceae s.l. A special feature is that the vascular bundle often does not end in the chalaza but may extend to the base of or into the outer or inner integument by forming several branches, or it may extend to the nucellus. In Picrodendraceae vascular bundles end at the base of the inner integument or in the chalaza (Berg 1975, Hakki 1985, this study). In Phyllanthaceae they may extend into the outer integument (in five genera out of 50 studied) (Tokuoka and Tobe 2001). In Euphorbiaceae s.str. there may be several vascular bundles in the inner integument (Singh 1965; Singh and Pal 1968; Tokuoka and Tobe 1998, 2002, pers. observ.), or one or several in the outer integument (Singh 1954, 1962; Tokuoka and Tobe 2002 2003, pers. observ.), or the vascular bundle may end in the nucellus or at the base of the nucellus (Johri and Kapil 1953, pers. observ.). In Putranjivaceae several vascular bundles extend into the outer integument (Singh 1970b, Tokuoka and Tobe 1999). Only in Pandaceae does the vascular bundle not extend beyond the chalaza (*Microdesmis*, pers. obs., Tokuoka and Tobe 2003). It appears that there is

a correlation between the presence of vasculature in the integuments and integument thickness (numbers of cell layers), as also discussed by Tokuoka and Tobe (1998, 2001, 2002, 2003). Thick integuments more often contain vascular bundles than thin integuments.

A nucellar cap has been recorded for many Euphorbiaceae s.l. (e.g. Schweiger 1905, Nair and Abraham 1963, Rao 1970, Bor and Kapil 1976, Kapil and Bhatnagar 1994, Sutter and Endress 1995). A nucellar beak is less often present, but occurs in all three larger families (Nair and Abraham 1963, Mukherjee and Padhye 1964, Singh 1968, Rao 1970, Bor and Bouman 1974, Bor and Kapil 1976, Kapil and Bhatnagar 1994, Sutter and Endress 1995). In Phyllanthaceae and Euphorbiaceae s.str. a nucellar beak that projects beyond the micropyle is more often present than in Picrodendraceae. In Putranjivaceae (Tokuoka and Tobe 1999) and Pandaceae (*Microdesmis*, pers. obs.) neither a nucellar cap nor a nucellar beak is formed.

The unusual character combination of nucellar beak (which may project far out of the micropyle), an extensive obturator and epitropous ovules is shared by the three larger families of Euphorbiaceae s.l. (but not Pandaceae and Putranjivaceae) (e.g. Sutter and Endress 1995, this study). The presence of obturators is always combined with epitropous ovules, and this correlation seems to have a functional basis, because in epitropous ovules the micropyle is turned away from the placenta and the obturator serves as an extended bridge to conduct pollen tubes from the placenta to the micropyle. Nevertheless, the combination is unusual and should also be discussed at the level of the order Malpighiales (see subsequent chapter).

Intra-ovarian hairs as reported here for five species of Picrodendraceae were not found in either Phyllanthaceae and Euphorbiaceae s.str. in our previous study (Sutter and Endress 1995) but are recorded now for both biovulate families (also for *Maesobotrya*, Phyllanthaceae; pers. obs.).

Female floral structure in Euphorbiaceae s.l. compared with "higher" Malpighiales in general.

In the phylogenetic study by Chase et al. (2002) all larger components of Euphorbiaceae s.l. (except Pandaceae) are part of a large clade within Malpighiales, which encompasses about half the total number of families in the order. To facilitate discussion this clade may be referred to as "higher Malpighiales" for the time being. It is composed of 4 major clades (in this discussion referred to as clade 1, 2, 3, 4). It has to be taken into account, however, that the relationships within Malpighiales (and within "higher" Malpighiales) are still poorly resolved (Davis et al. 2005, Wurdack and Davis 2005). Many of these families are small and poorly known and therefore have never been studied in detail as to their floral structural features. Within clade 1, Linaceae appear as sister to Picrodendraceae and both together are sister to a clade comprising Ochnaceae, Phyllanthaceae and Caryocaraceae. Clade 2 is sister to clade 1. It comprises the two subclades Chrysobalanaceae (including Euphroniaceae, Dichapetalaceae, Trigoniaceae) + Balanopaceae and Rhizophoraceae (including Erythroxylaceae) + Ixonanthaceae (see also Litt and Chase 1998). Clade 3 is sister to clade 1 + 2, and it includes the subclades Violaceae + Goupiaceae and Lacistemataceae + Ctenolophonaceae, and further Achariaceae, which are sister to the remainder of clade 3. Clade 4 is sister to clade 1 + 2 and clade 3. It contains Euphorbiaceae s.str. and Putranjivaceae + Irvingiaceae. We use this framework for discussion, although it is being modified by ongoing studies of different working groups and is at present in a state of flux.

Trimerous flowers are rare in core eudicots, although trimery of the gynoecium alone is common in many rosids (Endress 1996). In "higher" Malpighiales (other than Euphorbiaceae s.l.) the perianth is often 5-merous or less often 3–6-merous. Petals are mainly present. The gynoecium is 3-merous or varies between 2–5-merous. Although in Euphorbiaceae s.l. (see above) carpel number is similar as in other

"higher" Malpighiales, in Euphorbiaceae s.str., Phyllanthaceae, and Picrodendraceae the sepals are more often 3-merous and the petals are commonly absent (which contrasts with other "higher" Malpighiales). It should be considered that for unisexual and, in addition, apetalous flowers (most Euphorbiaceae s.l. but no other higher Malpighiales except Achariaceae) it is easier to become completely trimerous than it is for bisexual ones, because two or three fewer organ whorls are involved in the change (Endress 1996). Also, it is likely that this basic gynoecial trimery may more or less influence merism of the other whorls of floral organs (Endress 1996). Thus, for Euphorbiaceae s.l., and especially for Picrodendraceae there is a predominance of completely 3-merous flowers which is rare in other higher Malpighiales and eudicots.

The presence of an obturator is common in "higher" Malpighiales (no records in lower Malpighiales). It occurs not only in all Euphorbiaceae s.l. (excluding Pandaceae), but also in Ctenolophonaceae (Narayana and Rao 1971, 1978c), Dichapetalaceae (Sutter and Endress 1995), Erythroxylaceae (Boesewinkel and Geenen 1980), Irvingiaceae (Wiger 1935), Ixonanthaceae (Narayana and Rao 1966, Figs. 28, 37), Linaceae (Boesewinkel 1980, Narayana and Rao 1978b, Sutter and Endress 1995), Rhizophoraceae (Tobe and Raven 1987) and Trigoniaceae (Boesewinkel 1987). However, an obturator that intrudes into the micropyle appears to be a character that is special for Euphorbiaceae s.l. (excluding Pandaceae) since in other families of Malpighiales, it has only been observed in Linaceae (Boesewinkel 1980). Additionally, in Euphorbiaceae s.l. the obturator is often large, whereas in Ixonanthaceae and Rhizophoraceae it is medium-sized, in Ctenolophonaceae and Linaceae small to medium-sized, and in Dichapetalaceae, Erythroxylaceae, Irvingiaceae and Trigoniaceae small.

In Malpighiales most taxa have crassinucellar ovules but in "higher" Malpighiales, clade 1 + 2 has five families with at least, in part, incompletely tenuinucellar ovules (Ochnaceae, Linaceae, Chrysobalanaceae (incl. Dichapetalaceae, Trigoniaceae), Rhizophoraceae) or weakly crassinucellar ones (Ixonanthaceae) (review in Endress 2003, 2005). Situated between these taxa with incompletely tenuinucellar ovules are Picrodendraceae (and Phyllanthaceae) which have, together with the Euphorbiaceae s.str., only crassinucellar ovules. This may indicate that either the placement of Picrodendraceae in this clade is not correct or, alternatively, that there is more flexibility of transition between the two nucellus types than previously believed.

In the incompletely tenuinucellar ovules (at the mature embryo sac stage), the nucellus tip is destroyed by the growing embryo sac. In contrast, in the crassinucellar ovules of Malpighiales, the nucellus apex tends to enlarge by periclinal cell divisions of the epidermis (and subepidermal layers) as a nucellar cap. This is also the region, which may form a nucellar beak.

Interestingly, in Malpighiales a nucellar beak is only known from Euphorbiaceae s. str., Phyllanthaceae, and Picrodendraceae, and from two species of Malpighiaceae (Rao 1940, 1941). A nucellar beak (sometimes projecting far beyond the micropyle) is therefore a conspicuous feature uniting seemingly disparate families of Euphorbiaceae s.l.

The combination of nucellar beak, obturator and epitropous ovules, which may be unique for Euphorbiaceae s.l. (excl. Pandaceae and Putranjivaceae), is not found in other "higher" Malpighiales. Malpighiaceae, the only other family of the entire Malpighiales in which nucellar beaks have been recorded, also have epitropous ovules but no obturator. Among other "higher" Malpighiales, Ctenolophonaceae, Dichapetalaceae, Erythroxylaceae, Irvingiaceae, Ixonanthaceae, Linaceae, Rhizophoraceae and Trigoniaceae have the combination of epitropous ovules and obturator. Goupiaceae have epitropous ovules but no obturator (Loesener 1942).

A literature search through all families of Malpighiales showed that ovules with the inner integument thicker than the outer at the

mature embryo sac stage are common, not only in Euphorbiaceae s.l. but are also present in most of the families studied to date: Caryocaraceae (outer 2 or 3, inner 3 or 4 cell layers) (Dickison 1990); Chrysobalanaceae (6, 7) (Tobe and Raven 1984); Dichapetalaceae (4 or 5, 6–8) (Boesewinkel and Bouman 1980), Erythroxylaceae (3 or 4, 5 or 6) (Boesewinkel and Geenen 1980), Ixonanthaceae (2, 4) (Rao and Narayana 1965), Linaceae (2–3, 4–12) (Narayana 1963, Boesewinkel 1980, Sutter and Endress 1995), and Trigoniaceae (2 or 3, 4 or 5) (Boesewinkel 1987). In "lower" Malpighiales this is the case in Elatinaceae (2, 3) (Dathan and Singh 1971), Humiriaceae (2, 3) (Boesewinkel 1985), Hypericaceae (2, 4–6) (Schnarf 1914, Govindappa 1956, Rao 1957), and Malpighiaceae (2 or 3, 3 or 4) (Rao 1941).

The inner integument is thicker or both are equally thick in Passifloraceae and Salicaceae (Dathan and Singh 1973a, b; van Heel 1977; Kloos and Bouman 1979), both "lower" Malpighiales. Both integuments are equally thick in some Violaceae (3 cell layers) (Singh 1963) ("higher" Malpighiales) and Pandaceae (3 or 4 cell layers) (*Microdesmis*, pers. obs., Tokuoka and Tobe 2003) ("lower" Malpighiales). There is some lability in integument thickness, with the inner integument thicker or thinner at family level in Achariaceae (Dathan and Singh 1979; van Heel 1973, 1979; Steyn et al. 2001, 2002a, b) and Rhizophoraceae (Tobe and Raven 1987, 1988; Juncosa and Tobe 1988), both "higher" Malpighiales.

Only in Clusiaceae (Puri 1939, Prakash and Lau 1976, Lim 1984) and Podostemaceae (e.g. Jäger-Zürn 1967, Murguia-Sanchez et al. 2002) is the inner integument commonly thinner than the outer, both "lower" Malpighiales and closely related to each other.

In general, in bitegmic ovules of angiosperms the outer integument may become vascularized or, more rarely, the inner integument. Integumentary vascular bundles tend to occur more often in ovules that develop into large seeds, whereby the vascular system develops mainly during seed development (Bouman 1984). Vascular bundles in the inner integument or ending at the base of the inner integument may be a character which among Malpighiales only occurs in Euphorbiaceae s.str. and Picrodendraceae (probably not in Phyllanthaceae) and therefore, may be an exclusive character for Euphorbiaceae s.l. Further studies in the Malpighiales clades on the vascularisation will probably show that there is in fact more variation in this character than is currently recorded.

Female floral structure and systematic position of Picrodendraceae and Euphorbiaceae s.l.

In clade 1 (see preceding chapter), Linaceae share with Picrodendraceae anatropous, epitropous bitegmic ovules, an intruding obturator, axile placentation, secondary (false) septum, and inner integument that is thicker than the outer one. However, they differ in that the upper part of the ovary is unilocular, in having only weakly crassinucellar or incompletely tenuinucellar ovules, and in lacking a nucellar beak (e.g. Dorasami and Gopinath 1945, Narayana 1963, Narayana and Rao 1978b, Boesewinkel 1980, Sutter and Endress 1995, Endress 2003). Ochnaceae share anatropous, bitegmic ovules, however, the ovules are incompletely tenuinucellar and have an endothelium, at least in part with the integuments free only at the micropyle, and some have parietal placentation (Chikkannaiah and Mahalingappa 1974, Guédès and Sastre 1981, Narayana 1975). Caryocaraceae share axile placentation, anatropous, crassinucellar ovules, and inner integument thicker than outer integument (if bitegmic), but the ovules have the integuments free only in the upper region or are unitegmic, and are commonly campylotropous (Dickison 1990). For Phyllanthaceae, see preceding chapter.

In clade 2, Chrysobalanaceae share with Picrodendraceae anatropous ovules, inner integument thicker than outer, secondary (false) septum, but differ in incompletely tenuinucellar ovules with an endothelium (Tobe and Raven 1984). Dichapetalaceae share with Picrodendraceae an obturator, anatropous,

epitropous ovules, inner integument thicker than outer, but differ in incompletely tenuinucellar ovules (Boesewinkel and Bouman 1980, Sutter and Endress 1995). Trigoniaceae share with Picrodendraceae an obturator, anatropous, epitropous ovules, inner integument thicker than outer, micropyle formed by both integuments, but differ in parietal placentation and incompletely tenuinucellar ovules (Boesewinkel 1987) (however crassinucellar in *Trigoniastrum* and *Humbertiodendron*, according to a note without illustrations in Boesewinkel [1987]). Balanopaceae share with Picrodendraceae anatropous, crassinucellar ovules, but differ in the outer integument being thicker than the inner one, the presence of an endothelium and absence of an obturator (Merino Sutter and Endress 2003). Rhizophoraceae share with Picrodendraceae anatropous, crassinucellar ovules, vascular bundles in the outer integument, inner integument thicker than outer one, and an obturator, but differ in incompletely tenuinucellar ovules, and a zig-zag micropyle (Carey 1934; Tobe and Raven 1987 1988; Juncosa and Tobe 1988). Erythroxylaceae share with Picrodendraceae an obturator, anatropous, epitropous, crassinucellar ovules, inner integument thicker than outer one, but differ in the presence of an endothelium (Boesewinkel and Geenen 1980). Ixonanthaceae share with Picrodendraceae an obturator, anatropous, epitropous, presumably crassinucellar ovules, but differ in parietal placentation (Narayana and Rao 1966, 1978a).

In clade 3, Achariaceae share with Picrodendraceae anatropous, crassinucellar ovules, nucellar cap, but differ in parietal placentation, zig-zag micropyle, and vascular bundles in the outer integument (Bernhard 1999; Dathan and Singh 1979; van Heel 1973, 1977, 1979; Steyn et al. 2001, 2002a, b, 2003). Violaceae share with Picrodendraceae anatropous, bitegmic crassinucellar ovules, nucellar cap, but differ in parietal placentation, and zig-zag micropyle (Singh 1963). Goupiaceae and Lacistemataceae are poorly known in aspects that would be interesting for comparison (Krause 1925, Loesener 1942). Ctenolophonaceae share with Picrodendraceae an obturator, anatropous, epitropous, crassinucellar ovules, but differ in parietal placentation (Narayana and Rao 1971, 1978c).

In clade 4, Irvingiaceae share with Picrodendraceae an obturator, and anatropous to hemitropous, epitropous, crassinucellar ovules (Engler 1931, Wiger 1935). For Euphorbiaceae s.str. and Putranjivaceae see preceding chapter.

If all these families of the "higher" Malpighiales are compared, and especially compared to the families of Euphorbiaceae s.l. (except Pandaceae), they all share special floral features that support their relationships. But no special features emerge that would suggest closer relationhips with particular families of Euphorbiaceae s.l. On the contrary, the families of Euphorbiaceae s.l., especially Picrodendraceae, Phyllanthaceae, and Euphorbiaceae, still appear closely related from the point of view of floral structure. These three families share a combination of features that is unique within "higher" Malpighiales, including nucellar beak, obturator, crassinucellar, epitropous ovules, bifid stigmatic branches (rare but present also in Picrodendraceae), unisexual flowers, mostly without petals, floral trimery, explosive capsules with a coccal stage before rupture occurs (Berg 1975, Wurdack et al. 2004), and seeds with a caruncle, formed by the tip of the outer integument, which may function as a seed disjunctor and elaiosome (for Picrodendraceae, see Berg 1975, for other Euphorbiaceae s.l., see Tokuoka and Tobe 1998, 2002, 2003). It is unlikely that these unusual features are plesiomorphic for Malpighiales. Thus, the combination of these unusual features makes it likely that the three families are related within Malpighiales.

Should the three larger components of Euphorbiaceae s.l. later turn out to form a clade, what are its closest relatives? Malpighiaceae are of special interest from a structural point of view. Although not in "higher" Malpighiales and not appearing close to any

Euphorbiaceae s.l. in molecular phylogenetic studies, they share a number of special structural characters with Euphorbiaceae s.str. Malpighiaceae are the only additional family of Malpighiales, in which a nucellar beak was reported. The beak either protrudes out of the micropyle or at least into the micropyle (*Hiptage*, *Tristellateia*, *Banisteria, Stigmatophyllum,* Rao 1940, 1941; *Malpighia*, Stenar 1937; Singh 1961a, b). Further, some representatives of Malphighiaceae and Euphorbiaceae s.str. share the Penaea type of embryo sac development (which is otherwise very rare in angiosperms, and is not recorded in other Malpighiales), the presence of nectaries on leaves and dorsal side of sepals (Vogel 1974, Castro et al. 2001, Radcliffe-Smith 2001), unicellular, T-shaped trichomes (Cameron et al. 2001) and occurrence of latex in the relatively basal galphimioids of Malpighiaceae (Cameron et al. 2001, Davis et al. 2001, Vega et al. 2002) and in the three subfamilies Acalyphoideae, Crotonoideae and Euphorbioideae of Euphorbiaceae s.str. (Rudall 1987).

The morphological results from this study and from the literature do not support the proposed sister relationships of Picrodendraceae and Linaceae. Picrodendraceae share more morphological characters with Phyllanthaceae than with Linaceae or any other family of ''higher'' Malpighiales, and thus endorse more recent molecular studies, which showed weak (Wurdack 2002, Davis and Chase 2004, Wurdack et al. 2004) or stronger support for a sister relationship of Picrodendraceae and Phyllanthaceae (Wurdack and Davis 2005).

Comparative studies on reproductive structures in many poorly known families of the Malpighiales, and as a next step, comparisons between these families, are greatly needed. This should ideally go hand in hand with studies on extended molecular data sets. Both together could lead to a improved knowledge on the phylogeny and evolution of an exceedingly large and still highly enigmatic group of flowering plants (Endress and Friis 2006, Endress and Matthews 2006, Matthews and Endress 2006, Schönenberger and von Balthazar 2006).

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References

APG (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Berg R. Y. (1975) Fruit, seed and myrmecochorous dispersal in *Micrantheum* (Euphorbiaceae). Norw. J. Bot. 22: 173–194.

Bernhard A. (1999) Floral structure and development of *Ceratiosicyos laevis* (Achariaceae) and its systematic position. Bot. J. Linn. Soc. 131: 103–113.

Boesewinkel F. D. (1980) Development of ovule and testa of *Linum usitatissimum* L. Acta Bot. Neerl. 29: 17–32.

Boesewinkel F. D. (1985) The ovule and seed of *Humiria balsamifera* (Aubl.) St. Hil. Acta Bot. Neerl. 34: 183–191.

Boesewinkel F. D. (1987) Ovules and seeds of Trigoniaceae. Acta Bot. Neerl. 36: 81–91.

Boesewinkel F. D., Bouman F. (1980) Development of ovule and seed-coat of *Dichapetalum mombuttense* Engl. with notes on other species. Acta Bot. Neerl. 29: 103–115.

Boesewinkel F. D., Geenen J. (1980) Development of ovule and seed-coat of *Erythroxylum coca* Lamk. Acta Bot. Neerl. 29: 231–241.

Bor P. N., Bouman F. (1974) Development of ovule and integument in *Euphorbia milii* and *Codiaeum variegatum*. Phytomorphology 24: 280–296.

Bor J., Kapil R. N. (1976) Anatropy and ontogeny of the bitegmic ovule in *Chrozophora* A.H.L. Jussieu (Euphorbiaceae). Acta Bot. Neerl. 25: 385–400.

Bouman F. (1984) The ovule. In: Johri B.M. (ed.) Embryology of angiosperms. Springer, Berlin, pp. 123–157.

Cameron K. M., Chase M. W., Anderson W. R., Hills H. G. (2001) Molecular systematics of Malpighiaceae: evidence from plastid *rbc*L and *mat*K sequences. Amer. J. Bot. 88: 1847–1862.

Carey G. (1934) Further investigations on the embryogeny of viviparous seeds. Proc. Linn. Soc. New South Wales 59: 392–410.

Castro M. A., Vega A. S., Múlgura M. E. (2001) Structure and ultrastructure of leaf and calyx glands in *Galphimia brasiliensis* (Malpighiaceae). Amer. J. Bot. 88: 1935–1944.

Chase M. W., Zmarzty S., Lledó M. D., Wurdack K. J., Swensen S. M., Fay M. F. (2002) When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid *rbc*L DNA sequences. Kew Bull. 57: 141–181.

Chikkannaiah P. S., Mahalingappa M. S. (1974) Embryological studies in *Ochna squarrosa* Linn. Karnatak Univ. J. Sci. 19: 247–249.

Chopra S. (1970) Development of female gametophyte in *Sapium sebiferum* Roxb. Curr. Sci. 39: 17–18.

Corner E. J. H. (1976) The seeds of dicotyledons. Cambridge University Press, Cambridge.

Dahlgren R., Van Wyk A. E. (1988) Structures and relationships of families endemic to or centered in Southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 1–94.

Dathan A. S. R., Singh D. (1971) Embryology and seed development in *Bergia* L. J. Ind. Bot. Soc. 50: 362–370.

Dathan A. S. R., Singh D. (1973a) Development and structure of seed in *Tacsonia* Juss. and *Passiflora* L. Proc. Ind. Acad. Sci. B 77: 5–18.

Dathan A. S. R., Singh D. (1973b) Structure and development of ovule and seed in *Flacourtia indica* (Burm. f.) Merrill. Proc. Ind. Natl. Sci. Acad. B 39: 172–179.

Dathan A. S. R., Singh D. (1979) Structure and development of female gametophyte and seed in *Hydnocarpus laurifolia* (Dennst.) Sleumer. J. Ind. Bot. Soc. 58: 256–263.

Davis C. C., Chase M. W. (2004) Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. Amer. J. Bot. 91: 262–273.

Davis C. C., Anderson W. R., Donoghue M. J. (2001) Phylogeny of Malpighiaceae: evidence from chloroplast *ndh*F and *trn*L-F nucleotide sequences. Amer. J. Bot. 88: 1830–1846.

Davis C. C., Webb C. O., Wurdack K. J., Jaramillo C. A., Donoghue M. J. (2005) Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. Amer. Naturalist 165: E36-E65.

Dickison W. C. (1990) A study of the floral morphology and anatomy of the Caryocaraceae. Bull. Torrey Bot. Club 117: 123–137.

Dorasami L. S., Gopinath D. M. (1945) An embryological study of *Linum mysorense* Hyene. Proc. Ind. Acad. Sci. B 22: 6–9.

Endress P. K. (1994) Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.

Endress P. K. (1996) Homoplasy in angiosperm flowers. In: Sanderson M. J., Hufford L. (eds.) Homoplasy: the recurrence of similarity in evolution. Academic Press, San Diego, pp. 303–325.

Endress P. K. (2003) What should a "complete" morphological phylogenetic analysis entail? In: Stuessy T. F., Hörandl E., Mayer V. (eds.) Deep morphology: toward a renaissance of morphology in plant systematics. Gantner, Ruggell, pp. 131–164.

Endress P. K. (2005) Links between embryology and evolutionary flower morphology. Curr. Sci. 89: 749–754.

Endress P. K., Friis E. M. (2006) Rosids – Reproductive structures, fossil and extant, and their bearing on deep relationships: Introduction. Pl. Syst. Evol. (in press).

Endress P.K., Igersheim A. (2000) Gynoecium structure and evolution in basal angiosperms. Int. J. Pl. Sci. 161 (Suppl.): S211–S223.

Endress P. K., Matthews, M. L. (2006) First steps towards a floral structural characterization of the major rosid subclades. Pl. Syst. Evol. (in press).

Engler A. (1931) Simaroubaceae. In: Engler A., Prantl K. (eds.) Die natürlichen Pflanzenfamilien, 2nd edn., 19a. Engelmann, Leipzig, pp. 359–405.

Forman L. L. (1966) The reinstatement of *Galearia* Zoll. & Mor. and *Microdesmis* Hook. f. in the Pandaceae. Kew Bull. 20: 309–321.

Forman L. L. (1972). A synopsis of *Galearia* Zoll. & Mor. (Pandaceae). Kew Bull. 26: 153–165.

Forster P. I. (1995) *Sankowskya*, a new genus of Euphorbiaceae (Dissiliariinae) from the Australian wet tropics. Austrobaileya 4: 329–335.

Forster P. I. (1997a) A taxonomic revision of *Austrobuxus* (Euphorbiaceae: Dissiliariinae) in Australia. Austrobaileya 4: 619–626.

Forster P. I. (1997b) A taxonomic revision of *Dissiliaria* F. Muell. ex Baill. (Euphorbiaceae). Austrobaileya 5: 9–27.

Forster P. I., van Welzen P. C. (1999) The Malesian species of *Choriceras*, *Fontainea*, and *Petalostigma* (Euphorbiaceae). Blumea 44: 99–107.

Govindappa D. A. (1956) A morphological study of *Hypericum japonicum* Thbg. J. Mysore Univ. B 15: 69–79.

Guédès M., Sastre C. (1981) Morphology of the gynoecium and systematic position of the Ochnaceae. Bot. J. Linn. Soc. 82: 121–138.

Hakki M. I. (1985) Studies on West Indian plants 3. On floral morphology, anatomy and relationship of *Picrodendron baccatum* (L.) Krug & Urban (Euphorbiaceae). Bot. Jahrb. Syst. 107: 379–394.

Hayden W. J. (1994) Systematic anatomy of Euphorbiaceae subfamily Oldfieldiodeae. I. Overview. Ann. Missouri Bot. Gard. 81: 180–202.

Hayden W. J., Gillis W. T., Stone D. E., Broome C. R., Webster G. L. (1984) Systematics and palynology of *Picrodendron*: further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65: 105–127.

van Heel W. A. (1973) Flowers and fruits in Flacourtiaceae I. *Scaphocalyx spathacea* Ridl. Blumea 21: 259–279.

van Heel W. A. (1977) Flowers and fruits in Flacourtiaceae III. Some Oncobeae. Blumea 23: 349–369.

van Heel W. A. (1979) Flowers and fruits in Flacourtiaceae. IV. *Hydnocarpus* ssp., *Kiggelaria africana* L., *Casearia* ssp., *Berberidopsis corallina* Hook.f. Blumea 25: 513–529.

Huber H. (1991) Angiospermen: Leitfaden durch die Ordnungen und Familien der Bedecktsamer. Fischer, Stuttgart.

Igersheim A. (1993) The character states of the Caribbean monotypic *Strumpfia* (Rubiaceae). Nord. J. Bot. 13: 545–559.

Igersheim A., Cichocki O. (1996) A simple method for microtome sectioning of prehistoric charcoal specimens embedded in 2-hydroxyethyl methacrylate (HEMA). Rev. Palaeobot. Palynol. 92: 389–393.

Igersheim A., Endress, P. K. (1998) Gynoecium diversity and systematics of the paleoherbs. Bot. J. Linn. Soc. 127: 289–370.

Jäger-Zürn I. (1967) Embryologische Untersuchungen an vier Podostemaceen. Österr. Bot. Z. 114: 20–45.

Jensen U., Vogel-Bauer I., Nitschke M. (1994) Legumin-like proteins and the systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 160–179.

Johri B. M., Ambegaokar K. B., Srivastava P. S. (1992) Comparative embryology of angiosperms. Springer, Berlin.

Johri B. M., Kapil R. N. (1953) Contribution to the morphology and life history of *Acalypha indica* L. Phytomorphology 3: 137–151.

Juncosa A. M., Tobe H. (1988) Embryology of tribe Gynotrocheae (Rhizophoraceae) and its developmental and systematic implications. Ann. Missouri Bot. Gard. 75: 1410–1424.

Kajale L. B., Rao G. V. (1943) Pollen and embryo sac of two Euphorbiaceae. J. Indian Bot. Soc. 22: 229–236.

Kapil R. N. (1961) Some embryological aspects of *Euphorbia dulcis* L. Phytomorphology 11: 24–36.

Kapil R. N., Bhatnagar A. K. (1994) The contribution of embryology to the systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 145–159.

Kathriarachchi H., Hoffmann P., Samuel R., Wurdack K. J., Chase M. W. (2005) Molecular phylogenetics of Phyllanthaceae inferred from five genes (plastid *atp*B, *mat*K, 3'*ndh*F, *rbc*L, and nuclear *PHYC*). Molec. Phylogenet. Evol. 36: 112–134.

Kloos A., Bouman F. (1979) Case studies in aril development: *Passiflora suberosa* L. and *Turnera ulmifolia* L. Beitr. Biol. Pfl. 55: 49–66.

Krause K. (1925) Lacistemaceae. In: Engler A., Prantl K. (eds.) Die natürlichen Pflanzenfamilien, 2nd edn., 21. Engelmann, Leipzig, pp. 321–323.

Landes M. (1946) Seed development in *Acalypha rhomboidea* and some other Euphorbiaceae. Amer. J. Bot 33: 562–568.

Levin G. A., Simpson M. G. (1994) Phylogenetic implication of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

Lim A. L. (1984) The embryology of *Garcinia mangostana* L. (Clusiaceae). Gard. Bull. Singapore 37: 93–103.

Litt A., Chase M. W. (1998) The systematic position of *Euphronia*, with comments on the position of *Balanops*: an analysis based on *rbc*L sequence data. Syst. Bot. 23: 401–409.

Loesener T. (1942) Celastraceae. In: Engler A., Prantl K. (eds.) Die natürlichen Pflanzenfamilien, 2nd edn., 20b. Engelmann, Leipzig, pp. 87–197.

Maheshwari P. (1950) An introduction to the embryology of angiosperms. McGraw-Hill, New York.

Matthews M. L., Endress P. K. (2002) Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). Bot. J. Linn. Soc. 140: 321–381.

Matthews M. L., Endress P. K. (2004) Comparative floral structure and systematics in Cucurbitales (Corynocarpaceae, Coriariaceae, Tetramelaceae, Datiscaceae, Begoniaceae, Cucurbitaceae, Anisophylleaceae). Bot. J. Linn. Soc. 145: 129–185.

Matthews M. L., Endress P. K. (2005a) Comparative floral structure and systematics in Crossosomatales (Crossosomataceae, Stachyuraceae, Staphyleaceae, Aphloiaceae, Geissolomataceae, Ixerbaceae, Strasburgeriaceae). Bot. J. Linn. Soc. 147: 1–46.

Matthews M. L., Endress P. K. (2005b) Comparative floral structure and systematics in Celastrales (Celastraceae, Parnassiaceae, Lepidobotryaceae). Bot. J. Linn. Soc. 149: 129–194.

Matthews M. L., Endress P. K. (2006) Floral structure and systematics in four orders of rosids, including a broad survey of floral mucilage cells. Pl. Syst. Evol. (in press).

Matthews M. L., Endress P. K., Schönenberger J., Friis E. M. (2001) A comparison of floral structures of Anisophylleaceae and Cunoniaceae and the problem of their systematic position. Ann. Bot. 88: 439–455.

Meeuse A. D. J. (1990) The Euphorbiaceae auct. plur., an unnatural taxon. Eburon, Delft.

Meeuse A. D. J., Vinkenoog S., Vroege P. W. (1989) Anthecology of *Euphorbia* – preliminary studies. Acta Bot. Neerl. 38: 493–502.

Merino Sutter D., Endress P. K. (2003) Female flower and cupule structure in Balanopaceae, an enigmatic rosid family. Ann. Bot. 92: 459–469.

Metcalfe C. R., Chalk L. (1950) Anatomy of the dicotyledons, 1st edn. Clarendon Press, Oxford.

Mukherjee P. K., Padhye M. D. (1964) Contribution to the embryology of the genus *Phyllanthus* Linn. Proc. Natl. Acad. Sci. India, B. 34: 117–128

Murguia-Sanchez G., Novelo R. A., Philbrick C. T., Marquez-Guzman G. J. (2002) Embryo sac development in *Vanroyenella plumosa*, Podostemaceae. Aquat. Bot. 73: 201–210.

Nair N. C., Abraham V. (1963) A contribution to the morphology and embryology of *Micrococca mercurialis* Benth. J. Ind. Bot. Soc. 42: 583–593.

Nagaraj M. (1952) Floral morphology of *Populus deltoides* and *P. tremuloides*. Bot. Gaz. 114: 222–243.

Narayana L. L. (1963) A contribution to the floral anatomy and embryology of Linaceae. J. Ind. Bot. Soc. 43: 343–357.

Narayana L. L. (1975) A contribution to the floral anatomy and embryology of Ochnaceae. J. Jap. Bot. 50: 329–336.

Narayana L. L., Rao D. (1966) Floral morphology of Linaceae. J. Jap. Bot. 41: 1–10.

Narayana L. L., Rao D. (1971) Contributions to the floral anatomy of Linaceae II. Phytomorphology 21: 64–67.

Narayana L. L., Rao D. (1977) Contributions to the floral anatomy of Humiriaceae 6. J. Jap. Bot. 52: 145–153.

Narayana L L., Rao D. (1978a) Contributions to the floral anatomy of Linaceae (13). J. Jap. Bot. 53: 213–219.

Narayana L. L., Rao D. (1978b) Contributions to the floral anatomy of Linaceae (14). J. Jap. Bot. 53: 300–313.

Narayana L. L., Rao D. (1978c) Systematic position of Humiriaceae, Linaceae and Erythroxylaceae in the light of their comparative floral morphology and embryology - a discussion. J. Ind. Bot. Soc. 57: 258–266.

Narayanaswami S., Surinder S. (1959) Microsporogenesis and embryo sac development in *Casearia tomentosa* Roxb. Phyton 13: 133–144.

Nowicke J. W. (1994) A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.

Prakash N., Lau Y. Y. (1976) Morphology of *Ploiarium alternifolium* and the taxonomic position of *Ploiarium*. Bot. Not. 129: 279–285.

Puri V. (1939) Studies in the order Parietales II. A contribution to the morphology of *Garcinia*

livingstonii T. Anders. Proc. Ind. Acad Sci 9: 74–86.

Radcliffe-Smith A. (2001) Genera Euphorbiacearum. Cromwell Press, London (Kew).

Rao A. M. S. (1940) Studies in the Malpighiaceae. I. Embryo-sac development and embryogeny in the genera *Hiptage*, *Banisteria* and *Stigmatophyllum*. J. Ind. Bot. Soc. 18: 145–156.

Rao A. M. S. (1941) Studies in the Malpighiaceae. 2. Structure and development of the ovules and embryo-sacs of *Malpighia coccifera* Linn. and *Tristellateia australis* Linn. Proc. Natl. Inst. Sci. India 7: 393–404.

Rao D., Narayana L. L. (1965) Embryology of Linaceae. Curr. Sci. 34: 92–93.

Rao A. N. (1957) The embryology of *Hypericum patulum* Thunb. and *H. mysorense* Heyne. Phytomorphology 7: 36–45.

Rao A. N. (1964) Notes on the embryology of *Hevea brasiliensis* Muell. Curr. Sci. 33: 739–740.

Rao P. N. (1970) Euphorbiaceae. Bull. Indian Nat. Sci. Acad. 41: 136–141.

Rao P. N. (1976) Embryology of *Croton klotzschianus* Gamble. J. Ind. Bot. Soc. 55: 84–89.

Rao P. N., Rao D. S. (1976) Embryology of cassava. Proc. Ind. Natl. Sci. Acad. B 42: 111–116.

Rudall P. J. (1987) Laticifers in Euphorbiaceae – a conspectus. Bot. J. Linn. Soc. 94: 145–163.

Samuel R., Kathriarachchi H., Hoffmann P., Barfuss M. H. J., Wurdack K. J., Davis C. C., Chase M. W. (2005) Molecular phylogenetics of Phyllanthaceae: Evidence from plastid *mat*K and nuclear *PHYC* sequences. Amer. J. Bot. 92: 123–141.

Savolainen V., Fay M. F., Albach D. C., Backlund A., Van der Bank M., Cameron K. M., Johnson S. A., Lledó M. D., Pintaud J.-C., Powell M., Sheahan M. C., Soltis D. E., Soltis P. S., Weston P., Whitten W. M., Wurdack K. J., Chase M. W. (2000) Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull. 55: 257–309.

Schnarf K. (1914) Beiträge zur Kenntnis der Samenentwicklung einiger europäischer *Hypericum*-Arten. Sitzber. Akad. Wiss. Wien, Math.-Naturw. Kl., 123, Abt. I: 159–187.

Schönenberger J., von Balthazar (2006) Reproductive structures and phylogenetic framework of therosids – progress and prospects. Pl. Syst. Evol. (in press).

Schweiger J. (1905) Beiträge zur Kenntnis der Samenentwicklung der Euphorbiaceen. Flora 94: 339–379.

Simpson M. G., Levin G. A. (1994) Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Pl. Sci. 155: 313–341.

Singh B. (1961a) Studies in the family Malpighiaceae. II. Morphology of *Malpighia glabra* Linn. Hort. Adv. (Saharanpur) 5: 83–95.

Singh B. (1961b) Studies in the family Malpighiaceae. III. Development and structure of seed and fruit of *Malpighia glabra* Linn. Hort. Adv. (Saharanpur) 5: 145–155.

Singh D. (1963) Structure and development of ovule and seed of *Viola tricolor* L. and *Ionidium suffruticosum* Ging. J. Ind. Bot. Soc. 42: 448–462.

Singh R. P. (1954) Structure and development of seeds in Euphorbiaceae: *Ricinus communis* L. Phytomorphology 4: 118–123.

Singh R. P. (1962) Forms of ovules in Euphorbiaceae. In: Plant Embryology: a symposium. CSIR, New Delhi: pp. 124–128.

Singh R. P. (1965) Structure and development of seeds in *Codiaeum variegatum* Blume. J. Ind. Bot. Soc. 44: 205–210.

Singh R. P. (1968) Structure and development of seeds in Euphorbiaceae: *Melanthesa rhamnoides* Wt. Beitr. Biol. Pfl. 45: 127–133.

Singh R. P. (1970a) Structure and development of seeds in Euphorbiaceae: *Jatropha* species. Beitr. Biol. Pfl. 47: 79–90.

Singh R. P. (1970b) Structure and development of seeds in *Putranjiva roxburghii* Wall. J. Ind. Bot. Soc. 49: 99–105.

Singh R. P. (1972) Structure and development of seed in *Phyllanthus niruri* L. J. Ind. Bot. Soc. 51: 73–77.

Singh R. P., Pal A. (1968) Structure and development of seeds in Euphorbiaceae: *Dalechampia roezliana* Muell.-Arg. Tech. Comm. Nat. Bot. Gard. Lucknow 1968: 65–74.

Sleumer H. (1953) Las Flacourtiaceas argentinas. Lilloa 26: 5–56.

Soltis D. E., Soltis P. S., Chase M. W., Mort M. E., Albach D. C., Zanis M., Savolainen V., Hahn W. H., Hoot S. B., Fay M. F., Axtell M., Swensen S. M., Prince L. M., Kress W. J., Nixon K. C., Farris J. S. (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbc*L and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Stenar H. (1937) Zur Embryosackentwicklung einiger Malpighiazeen. Bot. Not. 1937: 110–118.

Steyn E. M. A., Van Wyk A. E., Smith G. F. (2001) A study of the ovule, embryo sac and young seed of *Guthriea capensis* (Achariaceae). S. Afr. J. Bot. 67: 206–213.

Steyn E. M. A., Van Wyk A. E., Smith G. F. (2002a) A study of ovule-to-seed development in *Ceratiosicyos* (Achariaceae) and the systematic position of the genus. Bothalia 32: 201–210.

Steyn E. M. A., Van Wyk A. E., Smith G. F. (2002b) Ovule, seed and seedling characters in *Acharia* (Achariaceae) with evidence of myrmecochory in the family. S. Afr. J. Bot. 68: 143–156.

Steyn E. M. A., Van Wyk A. E., Smith G. F. (2003) Embryology and systematic relationships of *Kiggelaria* (Flacourtiaceae). Bothalia 33: 199–206.

Stuppy W. (1996) Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Doctoral Dissertation, University of Kaiserslautern, Germany.

Sutter D., Endress P. K. (1995) Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. Bot. Jahrb. Syst. 116: 517–536.

van Tieghem P. (1898) Sur la structure de l'ovule et parti qu'on en peut tirer pour améliorer la classification. J. Bot. Paris 12: 197–220.

Tobe H., Raven P. H. (1984) An embryological contribution to systematics of the Chrysobalanaceae I. Tribe Chrysobalaneae. Bot. Mag. Tokyo 97: 397–411.

Tobe H., Raven P. H. (1987) The embryology and relationships of *Cassipourea* and *Sterigmapetalum* (Rhizophoraceae-Macarisieae). Opera Bot. 92: 253–264.

Tobe H., Raven P. H. (1988) Seed morphology and anatomy of Rhizophoraceae, inter- and intrafamilial relationships. Ann. Missouri Bot. Gard. 75: 1319–1342.

Tohda H. (1971) Embryological study on *Idesia polycarpa*. Sci. Rep. Tôhoku Univ. Ser. IV, 35: 231–237.

Tokuoka T., Tobe H. (1995) Embryology and systematics of Euphorbiaceae s. l.: a review and perspective. J. Pl. Res. 108: 97–106.

Tokuoka T., Tobe H. (1998) Ovules and seeds in Crotonoideae (Euphorbiaceae): structure and systematic implications. Bot. Jahrb. Syst. 120: 165–186.

Tokuoka T., Tobe H. (1999) Embryology of tribe Drypeteae, an enigmatic taxon of Euphorbiaceae. Pl. Syst. Evol. 215: 189–208.

Tokuoka T., Tobe H. (2001) Ovules and seeds in subfamily Phyllanthoideae (Euphorbiaceae): structure and systematic implications. J. Pl. Res. 114: 75–92.

Tokuoka T., Tobe H. (2002) Ovules and seeds in Euphorbioideae (Euphorbiaceae): structure and systematic implications. J. Pl. Res. 115: 361–374.

Tokuoka T., Tobe H. (2003) Ovules and seeds in Acalyphoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 116: 355–380.

Tokuoka T., Tobe H. (2005) Molecular phylogeny of Malpighiales and Euphorbiaceae, and evolution of ovule and seed coat characters. XVII International Botanical Congress, Abstracts, 219.

Vega A. S., Castro M. A., Anderson W. R. (2002) Occurrence and phylogenetic significance of latex in the Malpighiaceae. Amer. J. Bot. 89: 1725–1729.

Venkateswarlu J., Rao P. N. (1975) A contribution to the embryology of the tribe Hippomaneae of the Euphorbiaceae. J. Ind. Bot. Soc. 54: 98–103.

Vijayaraghavan M. R., Kaur D. (1966) Morphology and embryology of *Turnera ulmifolia* L. and affinities of the family Turneraceae. Phytomorphology 16: 539–553.

Vogel S. (1974) Ölblumen und ölsammelnde Bienen. Trop. Subtrop. Pflanzenwelt 7: 1–267.

Weber M., Igersheim A. (1994) "Pollen buds" in *Ophiorrhiza* (Rubiaceae) and their role in pollenkitt release. Bot. Acta 107: 257–262.

Webster G. L. (1975) Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

Webster G. L. (1987) The saga of the spurges: a review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

Webster G. L. (1994a) Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 3–32.

Webster G. L. (1994b) Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

Weckerle C. S., Rutishauser R. (2005) Fruit and seed development within Paullinieae (Sapindaceae). Bot. J. Linn. Soc. 147: 159–189.

Wiger J. (1935) Embryological studies on the families Buxaceae, Meliaceae, Simarubaceae

and Burseraceae. Doctoral Dissertation, University of Lund. Hakan Ohlsson, Lund.

Wurdack K. J. (2002) Molecular systematics and evolution of Euphorbiaceae sensu lato. Doctoral Dissertation. University of North Carolina, Chapel Hill, USA.

Wurdack K. J., Davis C. C. (2005) Progress in Malpighiales phylogeny: new insights from eight genes. XVII International Botanical Congress, Abstracts, 219.

Wurdack K. J., Hoffmann P., Samuel R., de Bruijn A., van der Bank M., Chase M. W. (2004) Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae sensu lato) using plastid *rbc*L DNA sequences. Amer. J. Bot. 91: 1882–1900.

Wurdack K. J., Hoffmann P., Chase M. W. (2005) Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbc*L and *trn*L-F DNA sequences. Amer. J. Bot. 92: 1397–1420.

Zhang, L.-B., Simmons M. P. (2006) Phylogeny and delimitation of the Celastrales inferred from nuclear and plastid genes. Syst. Bot 31: 122–137.

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